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Marine Flora and Fauna of the Northeastern United States Echinodermata: Crinoidea

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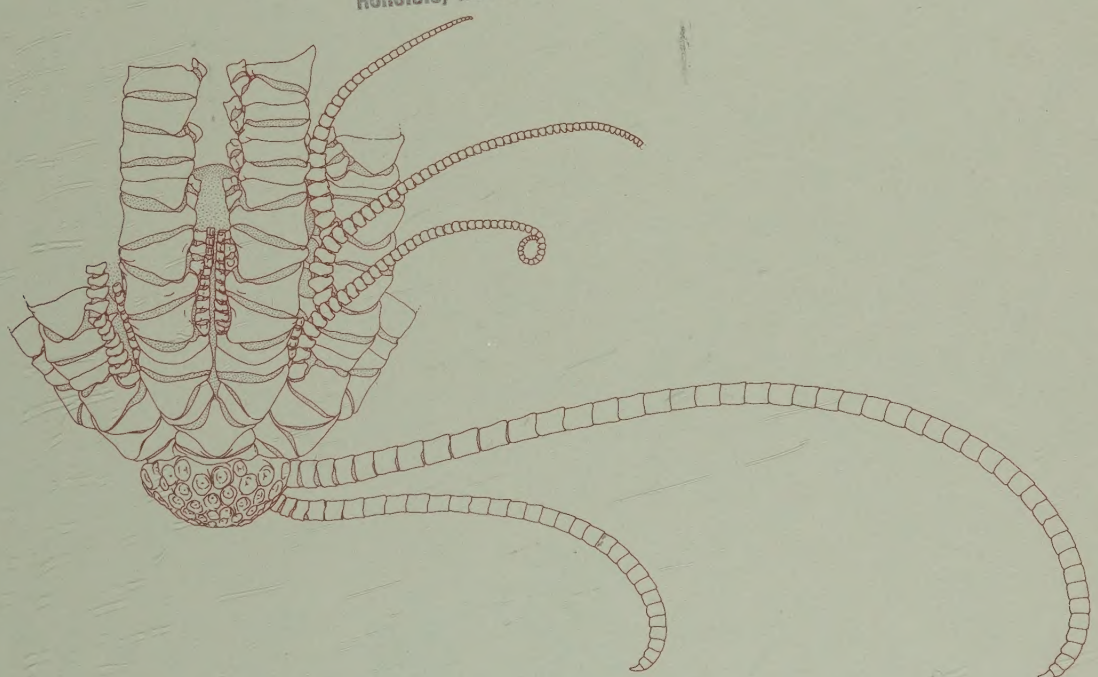

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Charles G. Messing
John H. Dearborn

August 1990

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Foreword

This NOAA Technical Report NMFS is part of the subseries "Marine Flora and Fauna of the Eastern United States" (formerly "Marine Flora and Fauna of the Northeastern United States"), which consists of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the eastern United States. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation. These manuals are intended for use by students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. They can often serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R.I. Smith, and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. Geographic coverage of the "Marine Flora and Fauna of the Eastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Florida, but can vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums.

The "Marine Flora and Fauna of the Eastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual, treating a separate major taxon, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist (with information, when available, on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

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Marine Flora and Fauna of the Northeastern United States Echinodermata: Crinoidea*

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ABSTRACT

The crinoid fauna of the continental margin (0–1500 m) of northeastern North America (Georgia to Canada) includes 14 species in 13 genera and 5 families. We introduce the external morphology and natural history of crinoids and include a glossary of terms, an illustrated key to local taxa, annotated systematic list, and an index. The fauna includes 2 species found no further south than New England and 8 that occur no further north than the Carolinas and Blake Plateau. *Comactinia meridionalis* (Agassiz) is the only species commonly found in shallow water (<50 m). No taxa are endemic to the area.

Introduction

The class Crinoidea includes the most exquisite members of the phylum Echinodermata and the only extant forms that bear a stalk. Forms known as sea lilies retain a stalk throughout their lives. Feather stars, or unstalked crinoids (order Comatulida), retain a stalk through a postlarval pentacrinoid stage, but discard it and take up a free existence as juveniles. All living forms have at least a superficial pentamerous radial symmetry and flexible featherlike arms. The arms bear reproductive organs and extensions of the water vascular system that serve for food capture and respiration. Crinoids orient in life with the oral surface uppermost, away from the substrate; both mouth and anus are on the oral surface.

Extant crinoids belong to the subclass Articulata which includes almost all post-Paleozoic taxa. Modern forms display a much narrower range of structural diversity than their far more numerous fossil forebears. The following discussion of morphology and natural history refers only to living species.

Crinoid taxonomy is not stable. Revisions at all taxonomic levels are either ongoing or needed and small numbers of new taxa are described each year. Between 600 and 700 extant species are generally recognized worldwide; about 70 occur in the North Atlantic. This paper includes crinoids found along the continental margin (0–1500 m) of northeastern North America (Georgia and northern Blake Plateau to Canada and Greenland). Several taxa currently known only as far north as the northern slopes of the Little Bahama Bank may eventually be found further north on the Blake Plateau and within the area covered by this manual. Included taxa belong to the order Bourgueticrinida (family Bathycrinidae) and order Comatulida (families Atelecrinidae, Comasteridae, Antedonidae, and Pentametrocrinidae).

External Morphology

Crinoid taxonomy is based chiefly on the endoskeleton of articulated calcareous plates, or **ossicles**, that composes a very large proportion of the whole animal (Figs. 1, 2, 3). This skeleton is far more obvious in crinoids than in other echinoderms. Most of the ossicles are covered only with a thin epidermis; they are clearly visible, although a dissecting microscope is generally required for recognition of diagnostic features.

The typical crinoid body is more or less lenticular and rests in a cuplike **calyx** composed of two circlets usually of five ossicles each (Figs. 1, 3). **Basal** ossicles, oriented interradially, form the aboral circlet. They are reduced in comatulids and generally not visible without dissection.

*Contribution No. 3 from the Deep Ocean Society, Miami, FL.

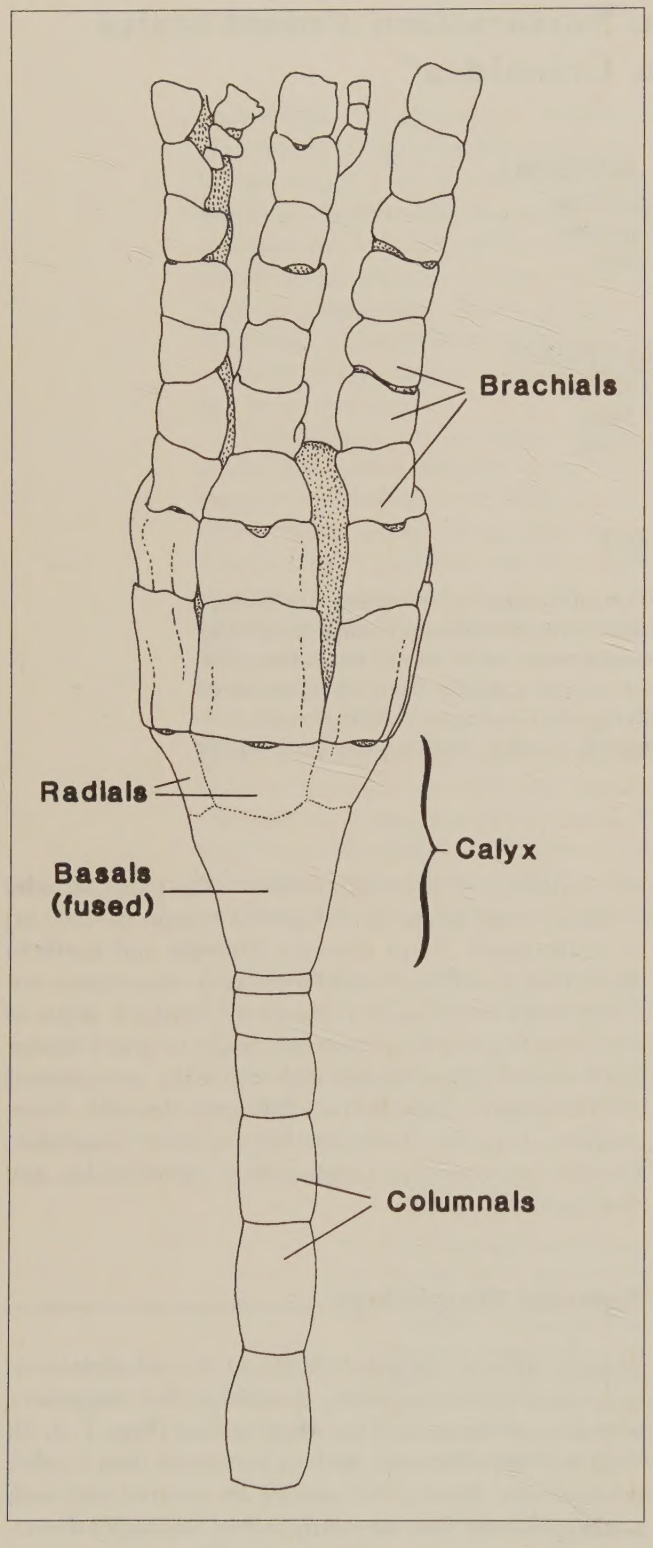


Figure 1
Lateral view of a stalked crinoid (order Bourgueticrinida) showing upper (proximal) portion of stalk, calyx, and bases of three rays.

Radial ossicles, associated with the five water vascular canals that radiate from the circumoral ring canal, form the second circlet. Radial and basal ossicles are immovably joined to each other. Both are at least partly obscured from external view by an aboral structure that supports the crinoid above the substrate. In sea lilies, it is a **stalk**. In comatulids, the calyx rests on a large modified ossicle, the **centrodorsal**, derived from the topmost segment of the postlarval stalk. (Phylogenetically, the centrodorsal may represent several fused stalk ossicles.) Centrodorsals range from disklike through hemispherical to cylindrical and usually bear numerous unbranched anchoring **cirri**. A typical cirrus is more or less prehensile, with the terminal segment modified as a claw and the penultimate bearing an opposing spine. Cirri range from short, robust and highly prehensile to long, slender and relatively straight. Rootlike segmented branching structures restricted to the stalk base of Bathycrinidae are also called cirri but are not homologous with cirri arising from the comatulid centrodorsal.

Each radial is the first, or most proximal, ossicle of a **ray**. Each ray consists of a complex, usually branched, series of ossicles that extends outward from the body, bearing an open **ambulacral groove** bordered by small fingerlike **tube feet**. Ossicles following the radials are called **brachials**. In rays that branch, each series of brachials leading from the radial to a branch point or from one branch point to another is termed a **division series** (or **brachitaxis**). Each division series is usually composed of two or four brachials and terminates with a modified **axillary** (or **axil**) ossicle that bears two articular faces distally. An axillary may thus bear two unbranched **arms**, two additional division series, or one of each. In unbranched rays, the arms extend from the radials. Young crinoids first develop five arms. Additional arms develop when one is shed and two grow back in its place. Many species have ten arms as a result; other chiefly tropical taxa have as many as 200.

Each arm bears smaller segmented unbranched appendages, **pinnules**, arranged in alternating series on either side. Arms, division series, and pinnules carry extensions of coelomic, nervous, and water vascular systems. Pinnules give the arms their characteristic featherlike appearance and are also the primary site of food collection. One or more pairs of pinnules near the arm base may be modified and lack an ambulacral groove. Such **oral pinnules** are often longer and more flexible or, in some families, more robust and spinelike than those succeeding. They are modified ostensibly for sweeping or protecting the oral surface. Oral pinnules are followed by several pairs of **genital pinnules** bearing the gonads. These rarely exhibit skeletal modifications; they are usually similar to the more distal, exclusively food-collecting pinnules.

In most modern crinoids, the cuplike structure of the calyx is lost; the calyx no longer surrounds the visceral

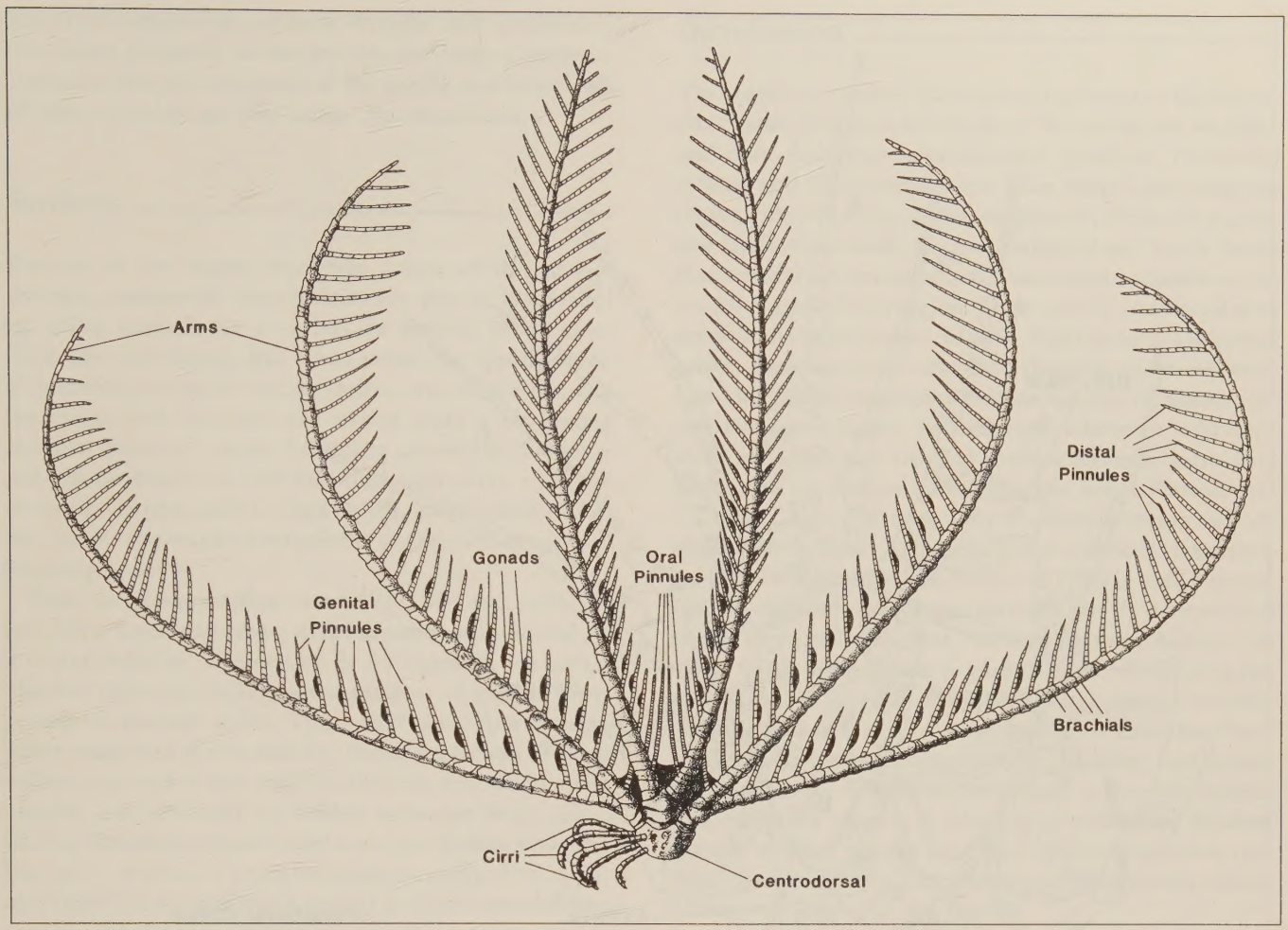


Figure 2
Lateral diagrammatic view of an unstalked crinoid or feather star (order Comatulida) showing centrodorsal with some cirri, and three rays. (Left- and right-hand rays show pinnules on only one side of each arm.)

mass. Instead, the viscera rest on top of the radial circlet and proximal ossicles of the rays. The oral surface of the visceral mass, the **tegmen**, or disk, is usually naked integument although it may be invested with small calcareous pieces. The tegmen bears both the anus, located at the apex of a small tube or papilla, and the mouth with its radiating ambulacral trunks. Portions of arms unattached to the visceral mass and distal to the tegmen are sometimes called free arms. The mouth is usually located centrally on the tegmen with the anus displaced to one side. In most Comasteridae the reverse is true.

Most articulations between successive ray ossicles contain both muscles and ligaments and are called **muscular articulations**. Moving from the aboral to the ambulacral surface of a typical brachial articular face, each articulation consists of a large aboral ligament, a transverse fulcral ridge, a pair of smaller ligaments and a pair of muscles. Ligaments and muscles insert into depressions, or fossae, in articular faces.

Exclusively ligamentary articulations have little or no flexibility. **Syzygies** are rigid articulations in which flat ridges radiating from the center of one articular face correspond with ridges on the other face. The ridges alternate with shallow grooves that also correspond on the two faces. Ridges and grooves do not interlock; the external appearance of the joint resembles a perforated line. Syzygies represent fracture points for arm autotomy and typically occur at regular, sometimes diagnostic intervals. **Synarthries** are ligamentary articulations characterized by a pair of semicircular ligaments separated by a fulcral ridge oriented vertically, that is, through the oral/aboral axis of the ray. Among comatulids, they are usually restricted to the middle joint in a division series of two ossicles (or the first joint in a division series of four ossicles), and the articulation between the first two arm brachials. The aboral surface around the joint of a pair of brachials united by synarthry is frequently swollen as a **synarthrial tubercle**. Such swellings are typical of many antedonids but are

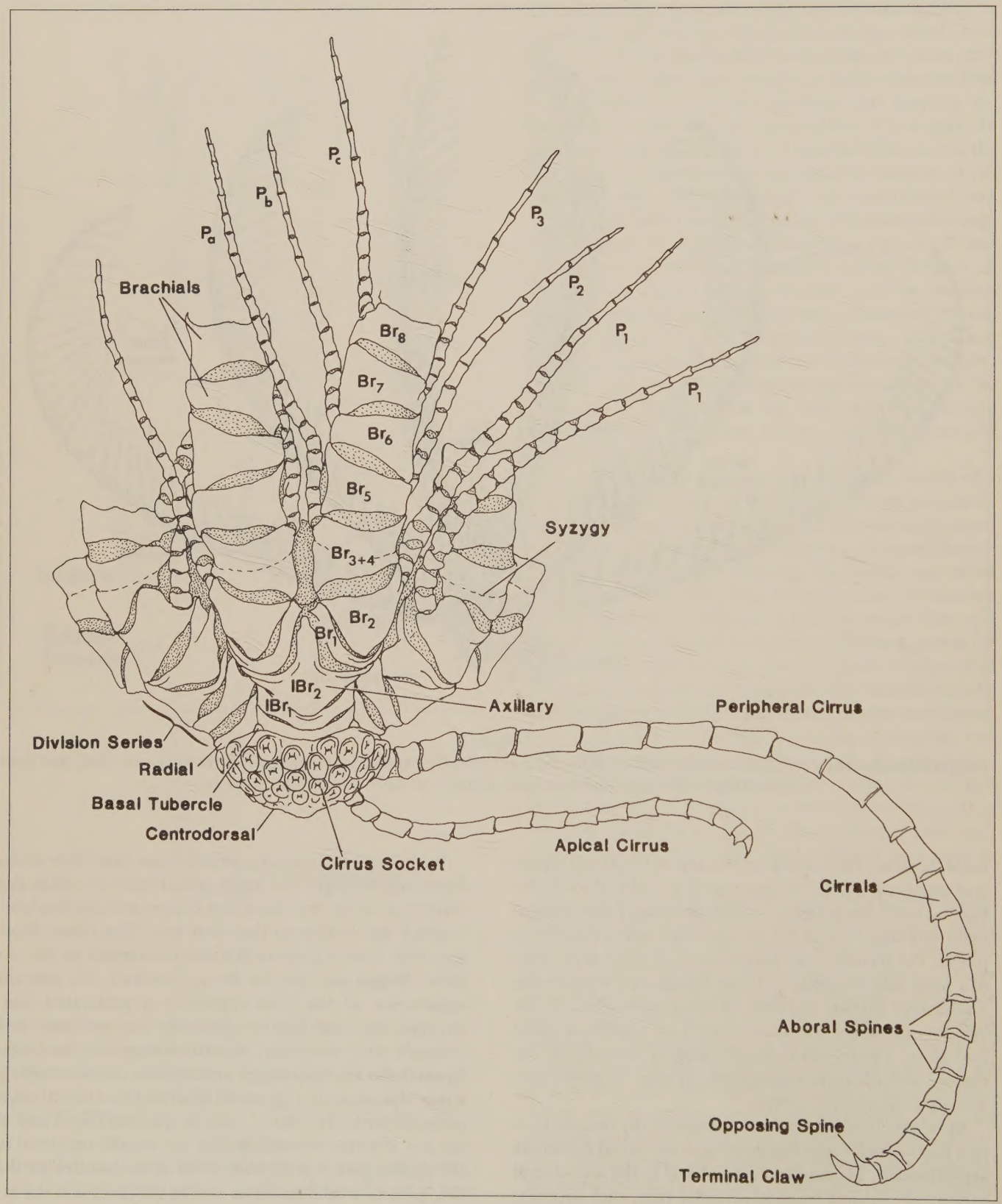


Figure 3
Lateral view of an unstalked crinoid (order Comatulida) showing centrodorsal, two cirri, and bases of three rays.

absent in comasterids. In both syzygies and synarthries, the ossicle proximal to the articulation lacks a pinnule. Hourglass-shaped columnals of the middle and lower stalk of Bathycrinidae are also united by synarthries.

Symbols

Because of the highly repetitive nature of the crinoid skeleton, taxonomic descriptions are greatly condensed by using symbols for a variety of skeletal parts. Considerable controversy has surrounded the identification of homologous ossicles across various crinoid groups, and the terms and symbols have varied quite a bit among authors. However, most of the taxa covered in this manual can be described with fair uniformity. We refer the reader to Ubaghs (1953), Clark (1970), and Breimer (1978) for more thorough discussions of crinoid structural homologies.

Basal ossicles are abbreviated B (pl. BB) and radials R (pl. RR). Each successive division series is indicated by a roman numeral followed by Br for brachial. An arabic number following indicates the number of ossicles composing the division series. Thus, IBr2 is the first division series composed of two ossicles; IIBr4 is a second division series composed of four ossicles. Individual division series ossicles are indicated by arabic subscript (e.g., IBr_2, $IIIBr_4$). Brachials of undivided arms are indicated as Br_1, Br_2, etc. A plus (+) sign indicates a syzygy. For example, IIBr4(3 + 4) indicates a second division series of four ossicles with the third and fourth joined by syzygy; Br_{9+10} indicates brachials nine and ten joined by syzygy. In *Conocrinus*, which has unbranched arms, we follow Gislén (1938) and Clark (1970) in numbering brachials from the first ossicle following the radial.

Pinnules are indicated by P. Arabic subscript numbers indicate successive exterior pinnules, that is, those along the outside of an arm; subscript lower case letters indicate interior pinnules (e.g., P_1, P_2, P_a, P_b). The interior side of an arm or division series is that side closest to the extrapolated median axis of the ray. In the ten-armed species included in this key (except *Atelecrinus* which has deficient pinnulation), Br_2 bears P_1, P_a is on the opposite side of Br_4 [Br_3 and Br_4 are joined by syzygy (Br_{3+4}) so there is no pinnule on Br_3], Br_5 bears P_2, and Br_6 bears P_b. Bathycrinids have relatively few pinnules that normally do not require specific enumeration.

In species descriptions, number of cirri is given in roman numerals and number of cirrals that compose a cirrus is given in arabic numerals. LW of cirrals indicates ratio of length to proximal width. Centrodorsal DH indicates ratio of greatest diameter to oral/aboral height. Arm LD indicates ratio of midradial ray length (L) from the distal margin of a radial to Br_{9+10}, to arm diameter (D) at Br_{3+4}.

Distribution

The region covered by this manual represents a depauperate, transitional area for crinoids. No species are endemic and only *Atelecrinus balanoides* and, possibly, *Trichometra cubensis* and *Conocrinus lofotensis* have ranges spanning the region. Three species, *Heliometra glacialis*, *Poliometra prolixa*, and *Hathrometra tenella*, represent a boreal and Arctic fauna that reaches its southern and westermost outposts in the northern part of this region. Over twenty additional taxa occur in the northeastern Atlantic. Eight species, *Democrinus conifer*, *Pentametrocrinus atlanticus*, *Comatilia iridometriformis*, *Comactinia echinoptera*, *Comactinia meridionalis*, *Comatonia cristata*, *Coccometra hagenii*, and *Zenometra columnaris*, represent elements of the rich tropical western Atlantic fauna that penetrates no further north than the Blake Plateau and Carolina Capes. Of these, only *P. atlanticus* occurs on both sides of the Atlantic. About two dozen additional taxa reach no further north than the Straits of Florida and Bahama Islands. Stalked crinoids are rare and poorly documented in the region. By contrast, the northeastern Atlantic (to about 2000 m) supports a varied fauna comprising ten species in four (possibly five) families; the tropical western Atlantic includes at least nine species in three families.

The majority of species occur on the outer continental shelf and slope. *Comactinia meridionalis* is the only species that normally occurs in shallow populations. Shallow records of other species are either unique (*Comatonia cristata*, *Coccometra hagenii*) or occasional (*Hathrometra tenella*, *Heliometra glacialis*) in the region.

Natural History

All extant crinoids are suspension feeders. They produce no respiratory/feeding current but rather rely on extrinsic water movement. For many years, our understanding of their ecology was both sketchy and fanciful. Crinoids were once supposed to sit on the sea floor with arms spread out in an upturned bowl, subsisting on a slow rain of detritus from above (Hyman 1955; Nichols 1962). It was also reported that they entangled prey with rhythmic scooping motions of their arms (Fell 1966). SCUBA and submersible observations have largely disproven both views (e.g., Meyer 1973; Macurda and Meyer 1974) and have also indicated that crinoids are not completely passive filter feeders.

Ecological studies of extant crinoids are largely descriptions of feeding postures and strategies because the food-gathering apparatus comprises such a large proportion of the animal's structure. It is critical to keep in mind, however, that the arms and pinnules that support the food-gathering apparatus also function in locomotion in most extant taxa. This dual obligation requires that the skeleton be rigid enough to stand erect against a passing current,

yet flexible enough to permit movement. The muscular articulations described above fit this requirement as follows: contractions of muscles on the ambulacral side of the fulcral ridges curl or roll the arms inward toward the mouth and flex pinnules toward the arm axis. When the muscles relax, the elasticity of the large antagonistic ligament extends arms and pinnules outward, allowing them to maintain an extended posture passively against a current for food gathering. Individual articulations have limited scope but an arm of over 200 segments or a pinnule with more than 50 may have great flexibility. Locomotion is achieved in comatulids and some stalked crinoids (Isocrinida) by arm crawling. Some comatulids are capable of swimming with graceful and coordinated arm undulations although they appear to do so only rarely.

In extant crinoids, the food-gathering apparatus functions as follows: each arm and pinnule bears an open ambulacral groove bordered by fingerlike **podia**, or **tube feet**—terminal extensions of the water vascular system. Unlike many asteroids, echinoids, and holothuroids, crinoid tube feet lack a terminal sucker. Tube feet are arranged in groups of three, each group including a short, medium, and long tube foot. The longest in each group, 0.5–0.85 mm in length (Meyer 1979), is the primary food gatherer. It is held out at a right angle and flicks passing food particles into the pinnule's ambulacral groove. Pinnule grooves run into arm grooves which converge like tributary rivers on the mouth. Captured particles are wrapped in mucous secretions and are transported mouthward by ciliary tracts that line the groove floor.

Food particle size depends chiefly upon tube-foot spacing and ambulacral groove width, and ranges from about 50 to 400 μm. Diets include a variety of protists (e.g., diatoms and other unicellular algae, foraminiferans, actinopods), invertebrate larvae, small crustaceans, and detrital particles.

All extant crinoids appear to use the same basic food-gathering system. Nevertheless, they do occupy a variety of niches based largely on flow regime preferences. Rheophilic forms prefer relatively strong or consistent, uni- or bi-directional flow. Most raise themselves above the substrate in order to intercept a satisfactory current. Sea lilies, of course, have the advantage of a stalk. Rheophilic comatulids typically cling to advantageous perches such as sponges, scleractinians, alcyonarians, projecting hard substrates and even sea lily stalks. Once above the substrate in a satisfactory "breeze," rheophiles arrange arms and pinnules in a variety of postures including parabolic and radial fans, and bi- and multi-layered vertical fans.

Rheophobic species typically conceal their calyx within crevices or under ledges on reefs and other rugged bottoms. Though still dependent upon water movement for food and gas exchange, they prefer a slower, multidirectional flow regime. Rheophobes typically extend their feeding arms with no particular orientation, but may direct successive pinnules at 90° angles to each other, a more efficient arrangement for intercepting particles that may come from any direction. Some deep-water taxa exposed to low flow velocities do arrange their rays in a bowl, apparently for gravitational interception of particles.

Some shallow-water comatulids remain exposed at all times; others are nocturnal and remain hidden during the day. Both groups include rheophilic and rheophobic forms. Species requiring exposed feeding perches are subject to predation by a variety of fishes and invertebrates (Mladenov 1983; Meyer et al. 1984; Meyer 1985) but attacks are rarely fatal. Predators usually crop one or more arms or pinnules, or remove the central visceral mass. The latter regenerates in less than a month. Defenses include diurnal seclusion (most teleosts that feed on calcareous prey are day-active); protection of the visceral mass by semicryptic behavior, development of large spinelike oral pinnules, or a dense thicket of arms and pinnules; incorporation of distasteful or toxic compounds; and crawling/swimming.

Crinoids host many parasites and commensals including pontoniine shrimp, cyclopoid copepods, isopods, cirripedes, gastropods, ophiuroids, clingfish, and myzostome polychaetes (the latter found almost exclusively on crinoids). These range from forms that use the crinoid as a convenient perch, through those that steal food from the ambulacral grooves, to parasites that feed directly on tissues and body fluids. Many match both color and pattern of the host crinoid.

Sexes are separate and almost uniformly identical. Reproductive modes among comatulids (sea lily development remains unknown) include broadcast spawning (the majority of species for which spawning is known), and both external and internal brooding. Free-swimming larvae, when present, are barrel-shaped, ciliated lecithotrophic doliolariae or vitellariae. With the exception of *Comatilia iridometriformis*, the twenty or so known internally brooding species are confined to middle and high southern latitudes. The latter include the only species with easily distinguishable sexes; females brood embryos in a marsupium, a pouch adjacent to the gonad on each genital pinnule.

Crinoids are difficult to maintain in aquaria because of their need for a continuous flow of plankton-laden water.

Preservation and Examination

Crinoids may be fixed in 10% buffered formalin and transferred to or preserved directly in 70% ethanol. Arm breakage is often a significant problem. Some species autotomize arms more easily than others. Similarly, some taxa respond to preservative by flexing their arms aborally, others orally. According to D. L. Meyer (Dep. Geology, Univ. Cincinnati, pers. commun., Jan. 1990), crinoids can be killed, often without major arm breakage, by immer-

sion, oral side down and arms outspread, in a shallow dish filled with 95% ethanol. Specimens are then transferred to 70% ethanol for storage. Colors tend to fade upon preservation, especially if alcohol is used.

Pinnules and cirri are best examined singly; they are most easily separated from an arm or centrodorsal of dried specimens by gentle prying with the tip of a fine forceps. This procedure normally destroys the articular face, however. In many-armed species with adjacent arms closely apposed, an entire arm or ray may have to be separated in order to examine the oral and genital pinnules. In taxa with numerous cirri, many cirri may have to be removed in order to examine centrodorsal and calyx.

Examination of individual ossicles and articular faces requires maceration in 5% sodium hypochlorite solution (i.e., commercial liquid bleach). External surfaces of sutures and articulations are best examined in dried specimens. However, dried (properly preserved) specimens become brittle; pinnules and arms of smaller specimens are particularly prone to breakage.

Glossary

Aboral. Away from or opposite to surface bearing mouth or ambulacrum.

Ambulacral. Toward, on, or associated with ambulacrum-bearing surface of ray, arm, or pinnule.

Ambulacral groove. Furrow in oral surface of tegmen, arms, and pinnules lined with tracts of cilia and serving to convey food to mouth.

Ambulacrum. Simple or branched, elongated area on oral surface of body, extending radially from mouth onto tegmen, arms, and pinnules, overlying radial water vascular canal and consisting of groove, marginal lappets, and podia.

Anal tube. Conical or cylindrical projection on oral surface bearing anus at its summit.

Arm. Unbranched, linear series of ossicles arising from radial ossicle of an unbranched ray, or from distalmost axillary of a branched ray.

Articular face (or facet). Usually sculptured surface of an ossicle serving as attachment site for ligaments or ligaments and muscles that join successive ossicles in a series.

Articulation (=Joint). Flexible to nearly immovable union of successive ossicles in a series.

Axillary (=Axil). Brachial bearing two distal articulations and representing the branching point of a ray.

Basal. Any of five interradial plates forming a circlet aboral to the radial circlet.

Basal ray. Any of five rodlike structures, modified parts of basal ossicles, lying interradially between radial circlet and centrodorsal of most comatulids (except Atelecrinidae); often visible as knobs at aboral corners of radials.

Basal tubercle (or knob). The outer tip of a basal ray when visible externally as a low triangle or rounded swelling at the aboral, interradial corner of a radial ossicle.

Brachial. Ossicle of an arm or division series.

Calyx. Cuplike central skeleton consisting (in recent species) of basal and radial circlets; reduced in comatulids.

Centrodorsal. Modified uppermost stalk ossicle attached to aboral surface of comatulids, retained after loss of larval stalk and commonly bearing cirri.

Cirral. Cirrus ossicle.

Cirrus (pl., cirri). Unbranched, usually hooklike, segmented appendage arising from stalk or centrodorsal; also refers to branched, segmented "roots" arising from disal end of stem in Bathycrinidae.

Cirrus socket. Articular face on centrodorsal or columnal for attachment of cirrus.

Column. Unbranched series of ossicles composing stalk or stem, exclusive of cirri, roots, or holdfast.

Columnal. Column ossicle.

Comb. Modification of distal pinnulars of oral pinnules producing comblike profile; in Comasteridae and a few species of Antedonidae.

Crown. In stalked species, the whole crinoid exclusive of stem.

Disk. Visceral mass that rests on the radial circlet and arm bases; sometimes its oral surface only (see ***tegmen***).

Distal. Referring to a direction or position away from the aboral/oral axis, that is, toward tips of rays, arms, and pinnules; also toward base of stalk.

Distal pinnule. Pinnules distal to genital and oral pinnules.

Division series (=Brachitaxis). Series of ossicles following a radial or axillary to and including the next axillary; series of ossicles between branches on a ray.

Genital pinnule. Gamete-bearing pinnules; usually distal to one or several pairs of modified oral pinnules.

Interradial. Oriented between rays, that is, between structures associated with radial water vascular canals.

Ligamentary articulation. Joints bearing only ligaments, lacking muscle fibers; examples include synarthry and syzygy.

Muscular articulation. Joint bearing both muscle fibers and ligaments; opposed articular faces usually characterized by a semicircular aboral ligament fossa, transverse fulcral ridge, axial canal, paired interarticular ligament fossae, and paired muscular fields. In comatulids, the great majority of arm articulations.

Oral. *(adj.)* Toward or on the mouth-bearing surface. *(n.)* Any of five interradially oriented plates forming circlet surrounding or covering mouth (absent in adult comatulids).

Oral pinnule. Any proximal pinnule differentiated from more distal pinnules in structure, function, or both.

Ossicle. Any single calcareous segment of crinoid skeleton (e.g., columnal, cirral, basal, radial, brachial, pinnular).

Pinnular. A pinnule ossicle.

Pinnule. Unbranched, segmented appendage usually arising from alternate sides of successive brachials (except axillaries and proximal ossicle of pair joined by syzygy).

Podia *(sing.,* ***podion)***. Tube feet; fine fingerlike projections of water vascular system that line ambulacral grooves and serve in food capture and respiration.

Proximal. Referring to direction or position toward aboral/oral axis, that is, toward base of ray, arm, or pinnule; also, toward top of stalk.

Radial. *(n.)* Most proximal ossicle of a ray, associated with any one of five radial water vascular canals that arise from the circumoral ring canal. *(adj.)* Associated or oriented with a ray.

Radial circlet *(* = ***Radial pentagon)***. Ring of five radials; sometimes fused into a cone or cup.

Ray. Radial ossicle together with all structures arising from it.

Rosette. Delicate, perforated structure formed of modified basal ossicles (excluding basal rods) located within radial circlet of comatulids (except Atelecrinidae).

Stalk *(* = **Stem***)*. Series of ossicles attached to aboral surface of crown and serving to anchor crown to and raise it above substrate; lost in adult comatulids.

Stereom. The fenestrated calcareous material of the crinoid endoskeleton.

Synarthrial swelling *(or* ***tubercle)***. Rounded or inflated thickening of aboral surface of ossicles joined by synarthry; lacking in most Comasteridae, present in many Antedonidae.

Synarthry. Ligamentary articulation in which opposed articular faces bear an aboral/oral-oriented fulcral ridge separating two lateral fossae for attachment of ligament bundles; permits limited side-to-side movement of joint.

Syzygial pair. Two ossicles joined by syzygy; the proximal ossicle lacks a pinnule.

Syzygy. Rigid ligamentary articulation in which ridges radiating from center of one articular face are apposed to corresponding ridges on the other face; visible externally as a perforated line; serves as breakage point for autotomy.

Tegmen. Oral surface of visceral mass bearing mouth, anus and trunks of ambulacra proximal to free portions of rays.

Key to the Crinoidea of the Continental Margin of Northeastern North America

1a Adult stalked, sessile; basal portion of stalk bears fine, rootlike branches; arms unbranched ..... **(Order Bourgueticrinida) 2**

1b Adult unstalked, sedentary; aboral centrodorsal bearing segmented, unbranched, usually prehensile cirri; centrodorsal variously shaped (conical, discoidal, hemispherical or cylindrical) ... **(Order Comatulida) 3**

2a(1a) Basal ossicles completely fused; sutures between basals not visible; sutures between radial ossicles visible or not; small and delicate; stalk usually no more than 50 mm in length; arms usually five (sometimes six or seven) in number; known chiefly from the north Atlantic, as far south as Massachusetts (possibly northern Florida) ..... ***Conocrinus lofotensis*** **(Fig. 4)**

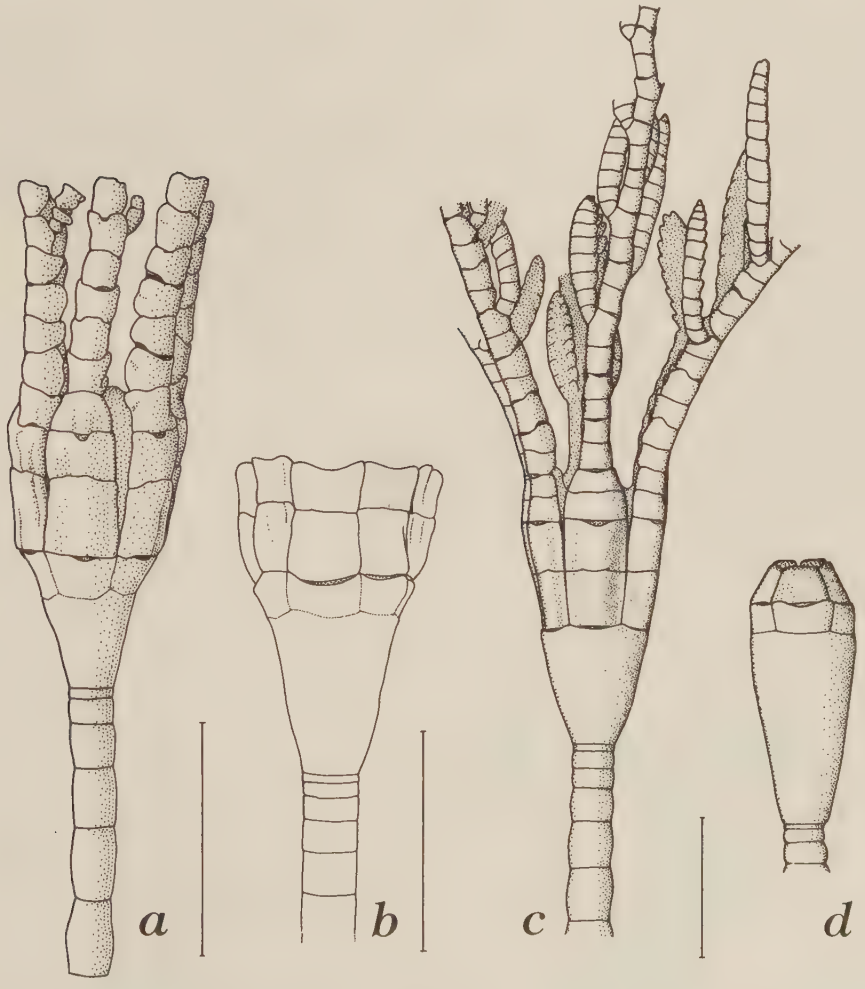


Figure 4

Conocrinus lofotensis. (***a*** through ***d***) Lateral views of upper stalk, calyx, and arm bases of three specimens. Scales: *a*, *c*, *d* = 2 mm; *b* = 5 mm. (*c* and *d* reprinted with permission from A. M. Clark, 1970).

2b(1a) Sutures between basal ossicles usually completely visible; sutures between radial ossicles completely visible; arms five; small and delicate to large and robust; stalk may exceed 200 mm in length; known chiefly from the Caribbean, as far north as the Blake Plateau ..... ***Democrinus conifer*** **(Fig. 5)**

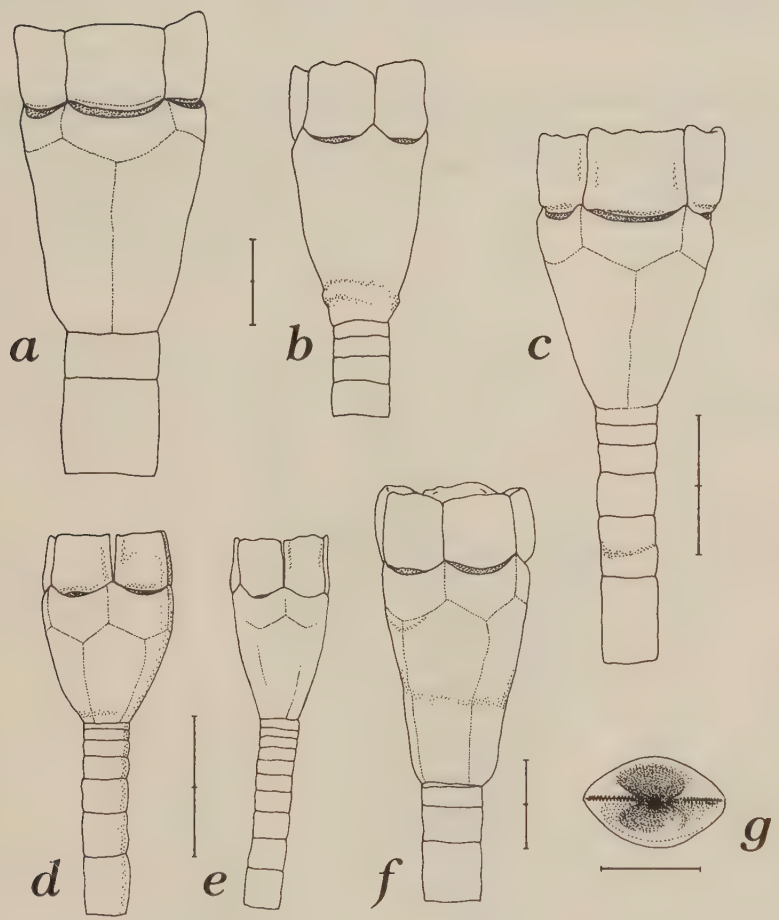


Figure 5
Democrinus conifer. (*a* through *f*) Lateral views of upper stalk, calyx, and arm bases (to the first brachial) of six specimens. (*g*) Distal columnal articulation. Scales: *a–f* = 2 mm; *g* = 1 mm.

3a(1b) Five undivided arms ..... ***Pentametrocrinus atlanticus*** **(Fig. 6)**

3b(1b) Ten arms; each ray with one division series of two ossicles joined by synarthry **4**

4a(3b) Basal ossicles form complete thin ring or pentagon usually visible externally as a narrow band completely separating centrodorsal from radial ossicles (but sometimes reduced to low, wide, interradial triangles); pinnules lacking on proximal 10–17 arm segments; centrodorsal almost always taller than wide, conical or with straight sides near base; cirrus sockets arranged in 10 alternating columns; each socket bears a pair of lateral, often aborally directed tubercles; cirri long slender and rarely retained.....
..... ***Atelecrinus balanoides*** **(Fig. 7)**

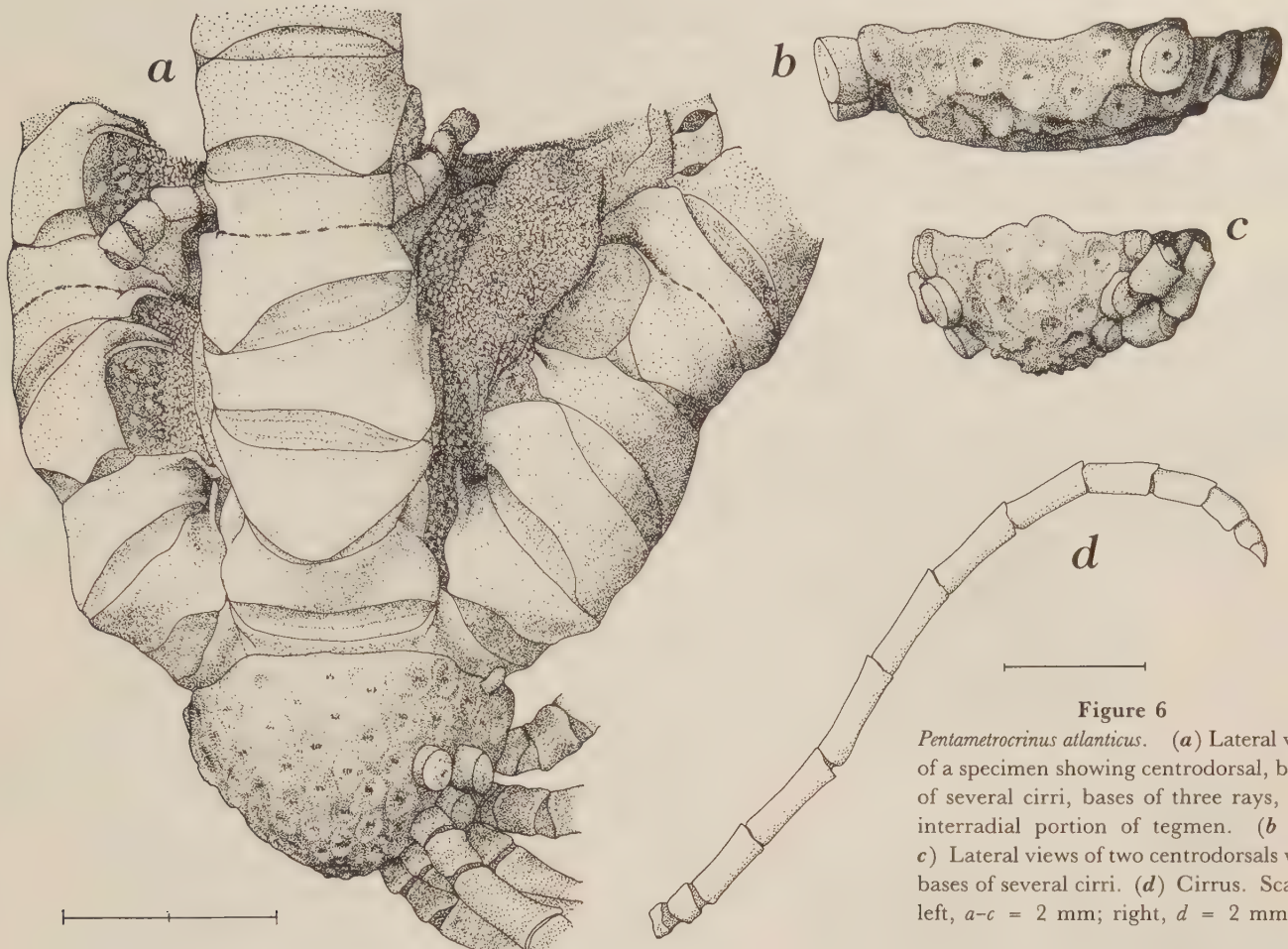


Figure 6
Pentametrocrinus atlanticus. (*a*) Lateral view of a specimen showing centrodorsal, bases of several cirri, bases of three rays, and interradial portion of tegmen. (*b* and *c*) Lateral views of two centrodorsals with bases of several cirri. (*d*) Cirrus. Scales: left, *a–c* = 2 mm; right, *d* = 2 mm.

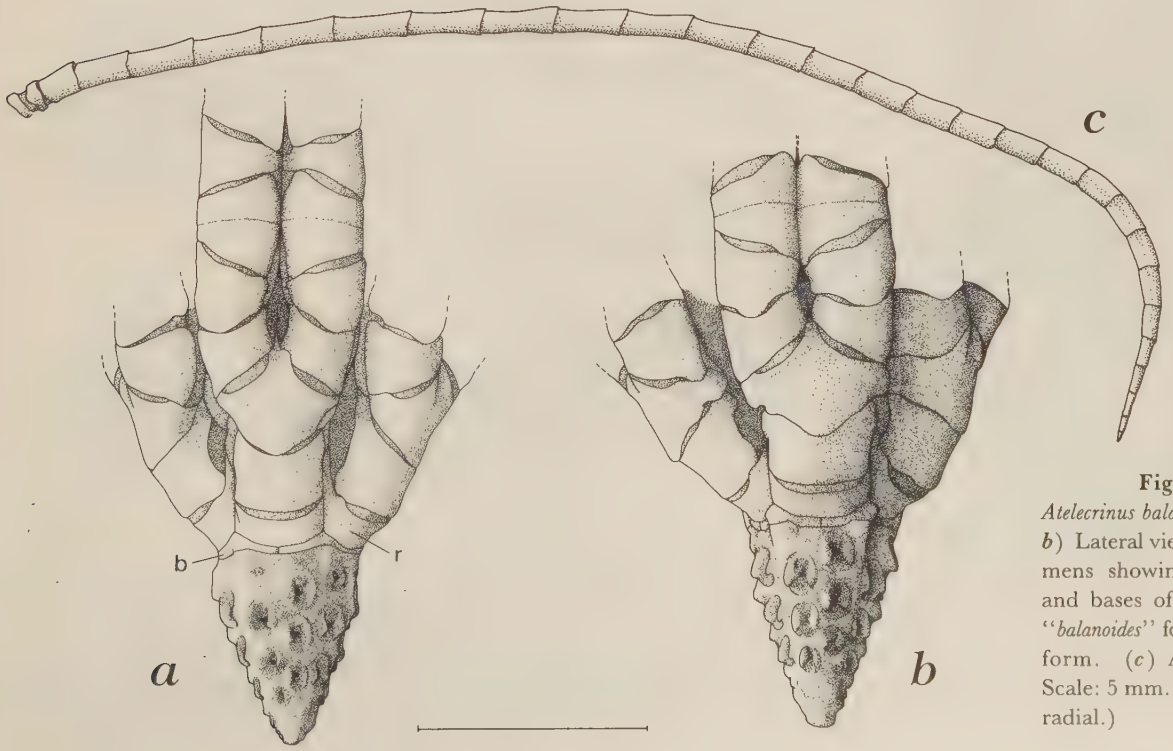


Figure 7
Atelecrinus balanoides. (*a* and *b*) Lateral views of two specimens showing centrodorsal and bases of three rays; *a*: "*balanoides*" form; *b*: "*helgae*" form. (*c*) Apical cirrus. Scale: 5 mm. (b = basal, r = radial.)

4b(3b) Basal ossicles reduced to an internal rosette with thin radiating rods sometimes visible externally as interradial tubercles; centrodorsal variously shaped; when conical, usually wider than tall; cirrus sockets without paired lateral tubercles; pinnules present on all or most proximal arm segments **5**

5a(4b) Distal segments of proximal one to four pairs of pinnules each bear a flat, round, triangular, or quadrate blade; blade-bearing pinnulars, taken together, form a comblike structure **6**

5b(4b) Proximal pinnules lacking comblike structure; pinnulars sometimes spinose distally **9**

6a(5a) Proximal pinnules all present; P_1 composed of 25–50 segments **7**

6b(5a) Second, third, and fourth pairs of pinnules (pinnules P_{2-4}, P_{b-d}) usually absent (P_2, P_b, or P_d occasionally present although not all together on the same arm of a specimen); P_1 of fewer than 25 segments; whole animal small and delicate with arms no longer than about 30 mm; unknown north of the Blake Plateau ..... *Comatilia iridometriformis* **(Fig. 8)**

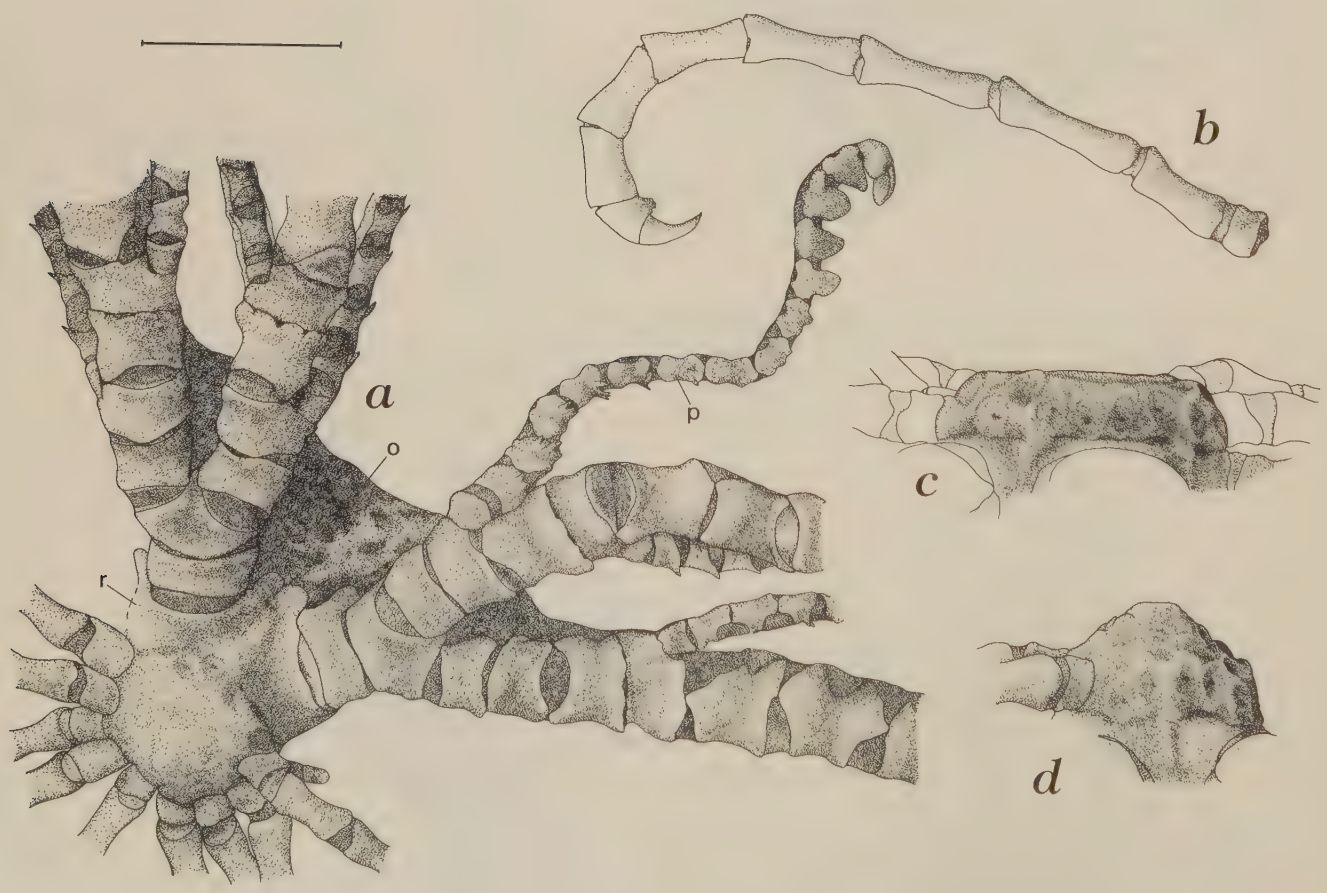


Figure 8

Comatilia iridometriformis. (***a***) Oblique aboral view showing centrodorsal and bases of cirri, and bases of two rays; (***b*** and ***c***) Centrodorsals (inverted); (***d***) Cirrus. Scale: 1 mm. (r = radial; o = oral surface; p = P_1).

7a(6a) Centrodorsal conical or hemispheric, almost covered with sockets; cirri slender and weakly curved; division series and first pair of arm segments strongly humped or swollen aborally (synarthrial tubercles); combs restricted to first pair of pinnules (sometimes only P_1; rarely also P_2), composed of large, round teeth and occupying all but basal third or fourth of pinnule; fifth to at least eighth brachial with an aboral spiny knob or keel; mouth central; unknown north of Cape Lookout, North Carolina ..... ***Comatonia cristata*** **(Fig. 9)**

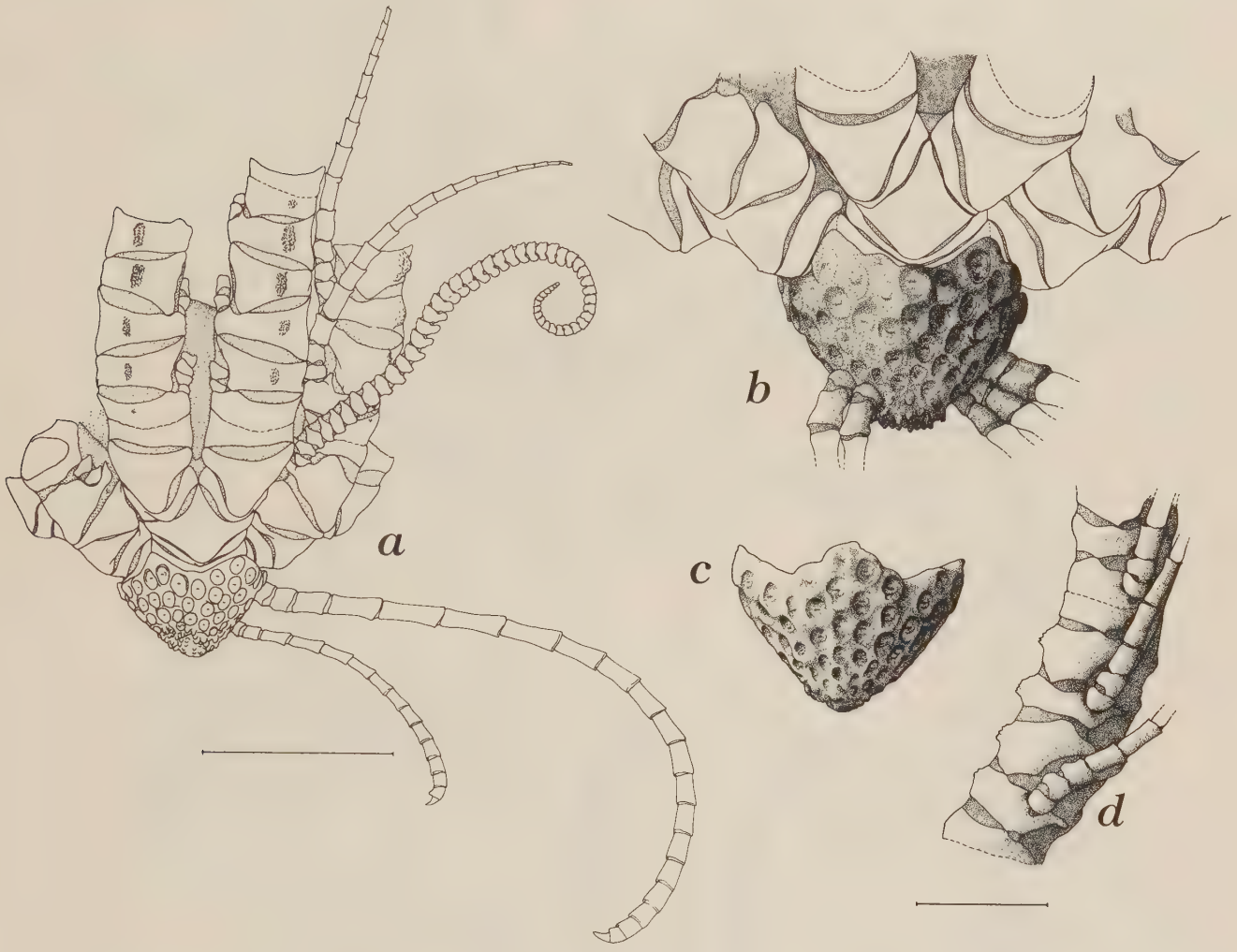


Figure 9

Comatonia cristata. (*a*) Lateral view showing centrodorsal with small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3; (*b*) Lateral view showing centrodorsal, bases of cirri and bases of three rays; (*c*) Centrodorsal; (*d*) Side view of arm base (Br_4–Br_{11}) showing spinose knobs. Scales: left, *a* = 5 mm; right, *b*, *c*, *d* = 2 mm..

7b(6a) Centrodorsal a flat disk or pentagon; cirri confined to lateral margins; cirri short, stout and usually curled terminally; division series and arm bases smoothly rounded, neither humped, swollen or keeled; comb on first, second, and sometimes third and fourth pinnule pairs, restricted to distal third or fourth of pinnule and composed of 3–11 rounded, triangular or quadrate teeth; comb teeth range from tall and conspicuous to low and weak; mouth displaced to one side of oral surface ..... **(Genus *Comactinia*)** 8

8a(7b) Comb usually present on P_{1-4}; middle comb teeth usually quadrate and often terminally notched; rounded keel usually present on basal segments of proximal pinnules; aboral distal margin of brachials lacks spines; color in life reddish flecked with yellow, with yellow pinnules; centrodorsal pale; ossicles retain pink color after dissociation in 5% sodium hypochlorite (NaOCl) solution; unknown north of Raccoon Key, South Carolina ..... ***Comactinia echinoptera*** **(Fig. 10)**

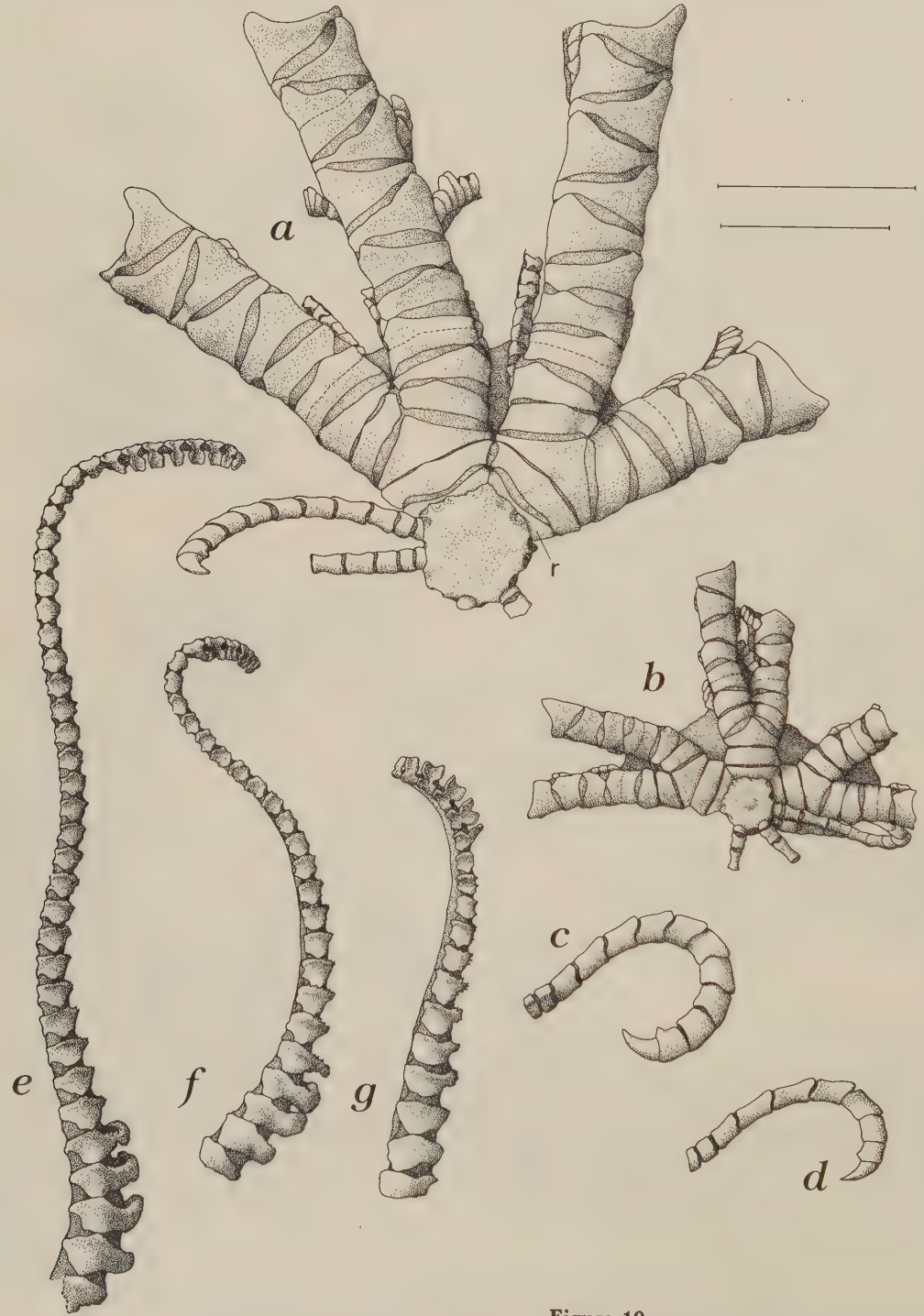


Figure 10

Comactinia echinoptera. (*a*) Aboral view showing centrodorsal and cirrus, and bases of two rays; (*b*) Aboral view of small specimen showing centrodorsal and cirrus, and bases of three rays; (*c* and *d*) Cirri; (*e*) P_1; (*f*) P_2; (*g*) P_3. Scales: upper, *a–d* = 5mm; lower, *e–g* = 2 mm. (r = radial.)

8b(7b) Comb on P_{1-2} (sometimes P_3 and P_4); teeth rounded or triangular, weak or strong; basal keels absent; middle segments of proximal pinnules with spiny rims that may develop into strong, spiny flanges; aboral distal margin of brachials finely spiny; color yellow, red, purple, brown, or a combination; all color lost upon dissociation in 5% sodium hypochlorite (NaOCl) solution; unknown north of Cape Lookout, North Carolina ..... *Comactinia meridionalis* **(Fig. 11)**

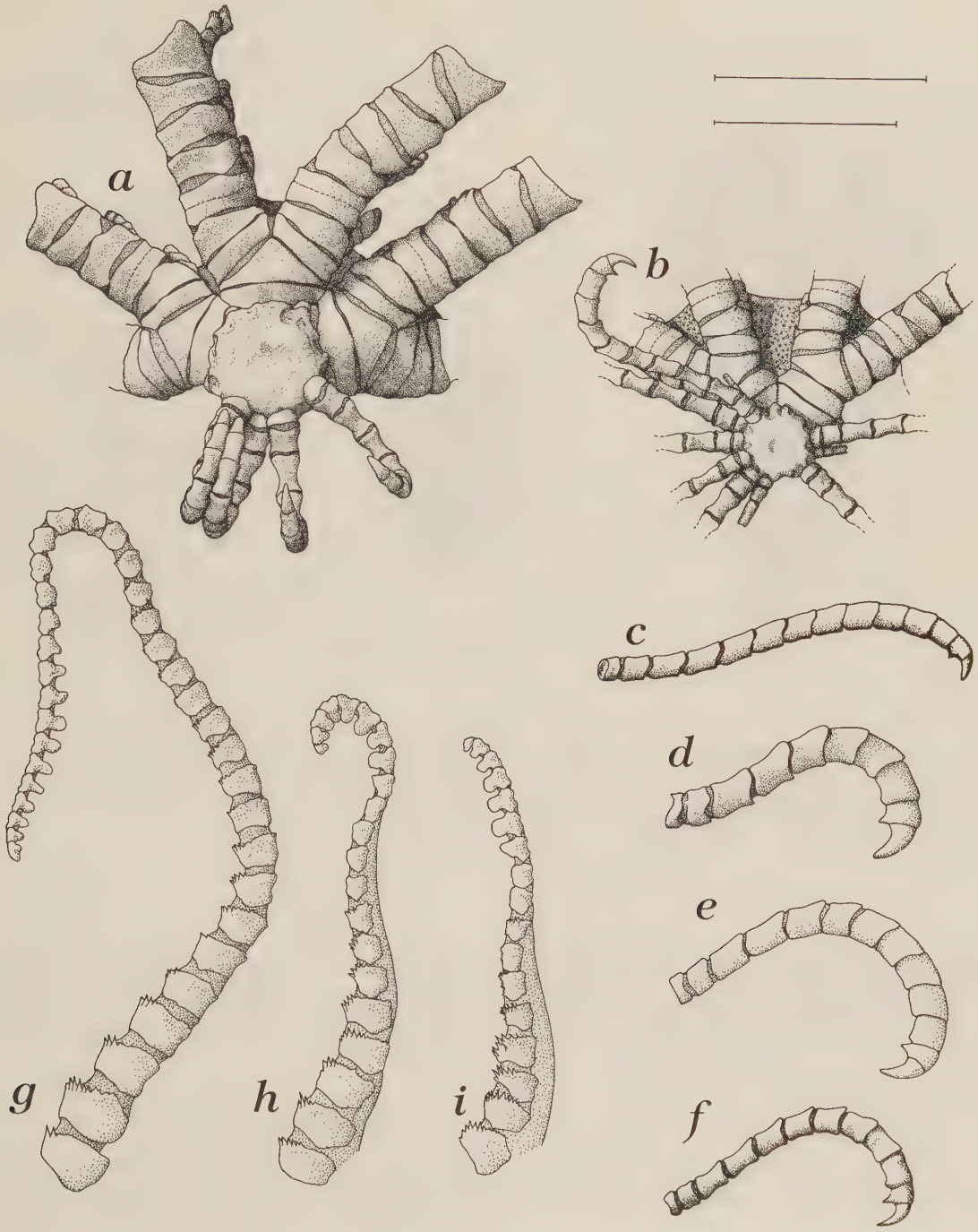


Figure 11

Comactinia meridionalis. (*a*) Aboral view showing centrodorsal and cirri, and bases of three rays; (*b*) Aboral view of small specimen showing centrodorsal and cirrus, and bases of two rays; (*c* through *f*) Cirri; (*g*) P_1; (*h*) P_2; (*i*) P_3. Scales: upper, *a–f* = 5 mm; lower, *g–i* = 2 mm.

9a(5b) Centrodorsal taller than wide, cylindrical, or truncated conical, with five interradial ridges separating paired alternating columns of cirri; centrodorsal apex often excavated; division series and arm base ossicles usually bear fringe of long glassy spines; proximal pinnules compressed, with all segments longer than wide; unknown north of Blake Plateau ..... ***Zenometra columnaris*** **(Fig. 12)**

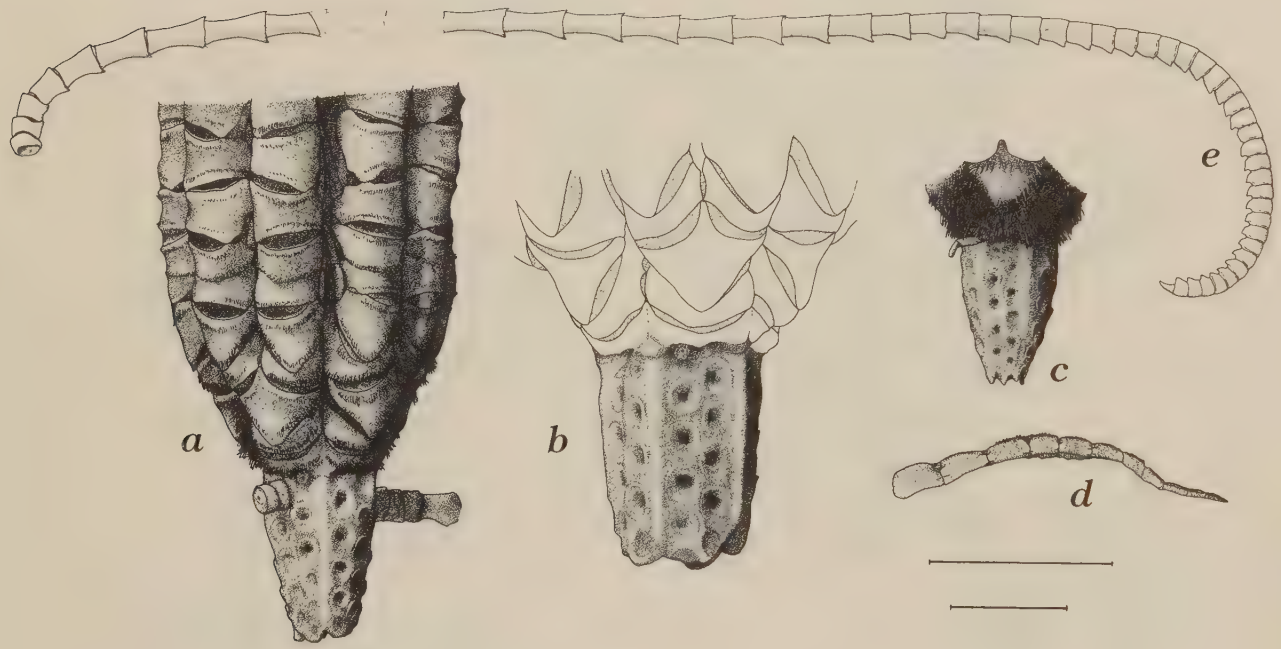


Figure 12

Zenometra columnaris. (*a*) Lateral view showing centrodorsal and bases of cirri, and bases of four rays; (*b*) Lateral view showing centrodorsal and bases of three rays; (*c*) Lateral view showing centrodorsal, base of immature cirrus, and bases of three rays (covered with spines); (*d*) P_1; (*e*) Cirrus. Scales: upper, *a–c*, *e* = 5 mm; lower, *d* = 5 mm.

9b(5b) Centrodorsal rounded conical or hemispherical, as wide as tall or wider, lacking interradial ridges; cirri in closely spaced spiral rows (sometimes in columns as well or so crowded that no pattern is visible); proximal pinnules not markedly compressed and with first two or more segments short or squarish ... **10**

10a(9b) Centrodorsal flattened hemispherical to rounded conical, from 1.5 to more than 2.0 times wider than tall, with a smooth apical area lacking cirrus sockets; P_1 (and sometimes one or more subsequent pinnules) very flexible, usually of 35 or more segments, even distal pinnulars short—no more than twice as long as wide; P_2 similar in length to P_1 (sometimes 3/4 as long as P_1, rarely longer) **11**

10b(9b) Centrodorsal conical to rounded conical, no more than 1.5 times wider than tall, usually about as wide as tall, almost completely covered with sockets or with spiny or papillose apex; P_1 rather stiff, rarely with more than 35 segments; middle and distal pinnulars thin, elongated and up to several times longer than wide, usually with expanded spiny distal ends; P_1 usually 2–4 times longer than P_2 ..... **12**

11a(10a) Very large; arms often exceeding 200 mm in length and 3 mm in basal width; peripheral cirri up to 70 mm long, usually with 44–55 cirrals none of which are more than twice as long as their narrowest width; P_{1-3} similar, of many short segments; P_1 usually 15–25 mm long, of 42–54 (up to 82) segments; unknown south of Georges Bank, Massachusetts ..... ***Heliometra glacialis*** **(Fig. 13)**

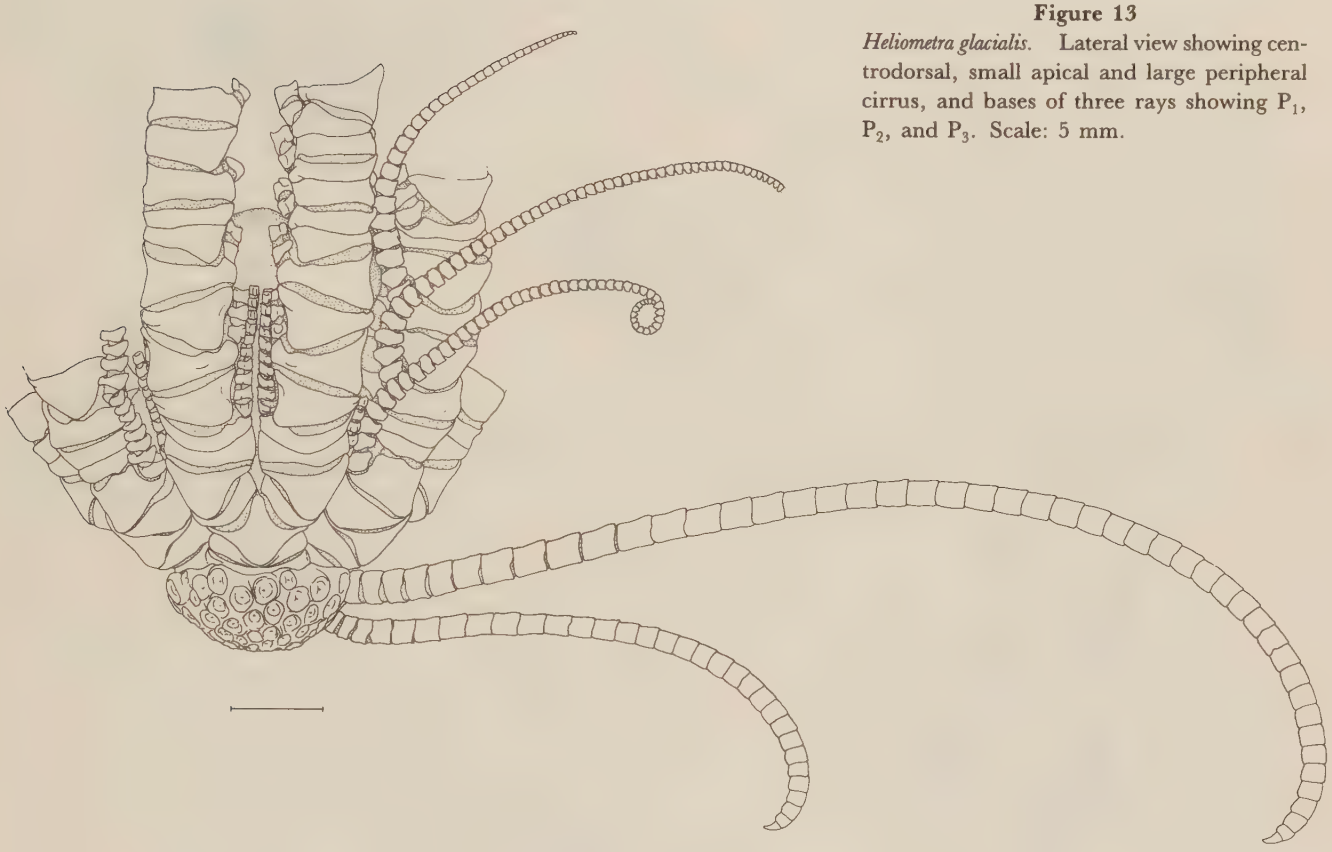


Figure 13
Heliometra glacialis. Lateral view showing centrodorsal, small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3. Scale: 5 mm.

11b(10a) Much smaller; maximum arm length 75 mm and basal width 1.4 mm; peripheral cirri rarely more than 15 mm long, usually of 15–20 segments; longest cirrals 2.5–3.0 times longer than their narrowest width; P_1 usually 8–10 mm long, of 30–43 short segments; P_{2-3} of far fewer, longer segments (P_2 may occasionally resemble P_1); unknown north of Cape Lookout, North Carolina ..... ***Coccometra hagenii*** **(Fig. 14)**

12a(10b) Ossicles of division series and arm bases laterally separated and not laterally thickened or flattened, distal aboral margins not everted and spiny; P_1 two to four times longer than P_2; longest cirrals three to five times longer than their narrowest width **13**

12b(10b) Ossicles of division series and arm bases laterally thickened, flattened and closely appressed; P_1 no more than about twice as long as P_2; longest cirrals no more than three and a half times longer than their narrowest width ..... (***Trichometra cubensis***) **14**

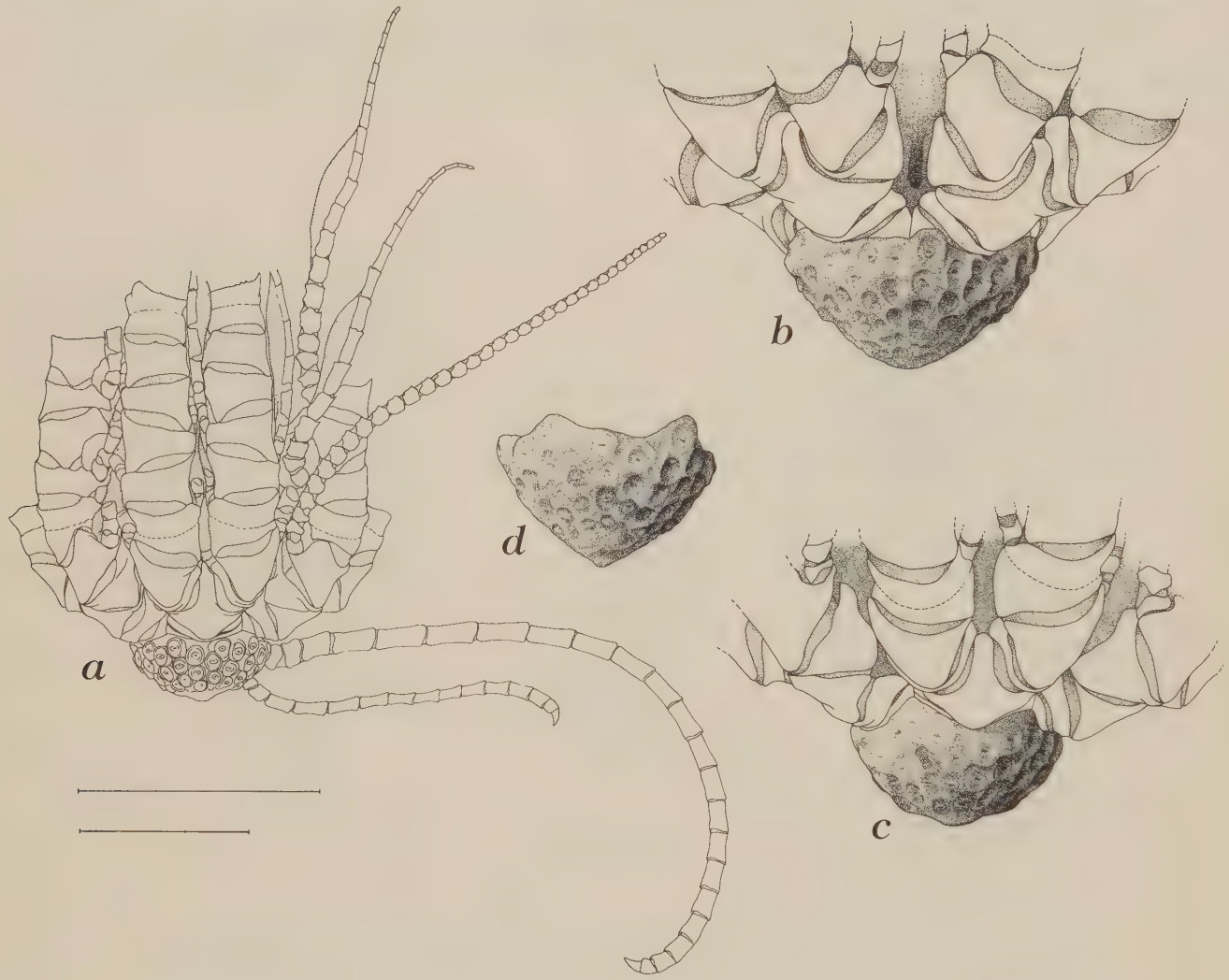


Figure 14

Coccometra hagenii. (*a*) Lateral view showing centrodorsal, small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3 (P_2 and P_3 bear gonads); (*b* and *c*) Lateral views showing centrodorsal and bases of rays; (*d*) Centrodorsal. Scales: upper, *a* = 5 mm; lower, *b–d* = 2 mm.

13a(12a) Large cirrus sockets arranged in distinct vertical columns as well as spirally; cirri usually 30–60 mm long and composed of 30–50 segments; arms usually with four muscular articulations between successive syzygies; P_1 less than half the length of peripheral cirrus, with 5–7 short basal segments; unknown south of Greenland ..... ***Poliometra prolixa*** **(Fig. 15)**

13b(12a) Small cirrus sockets in crowded spiral rows (columns, if present, indistinct); cirri usually 25–30 mm long and composed of 20–30 (maximum 33) cirrals; arms usually with three muscular articulations between successive syzygies following Br_{9+10}; P_1 at least half as long as peripheral cirrus, with 3–5 short basal segments ..... ***Hathrometra tenella*** **(Fig. 16)**

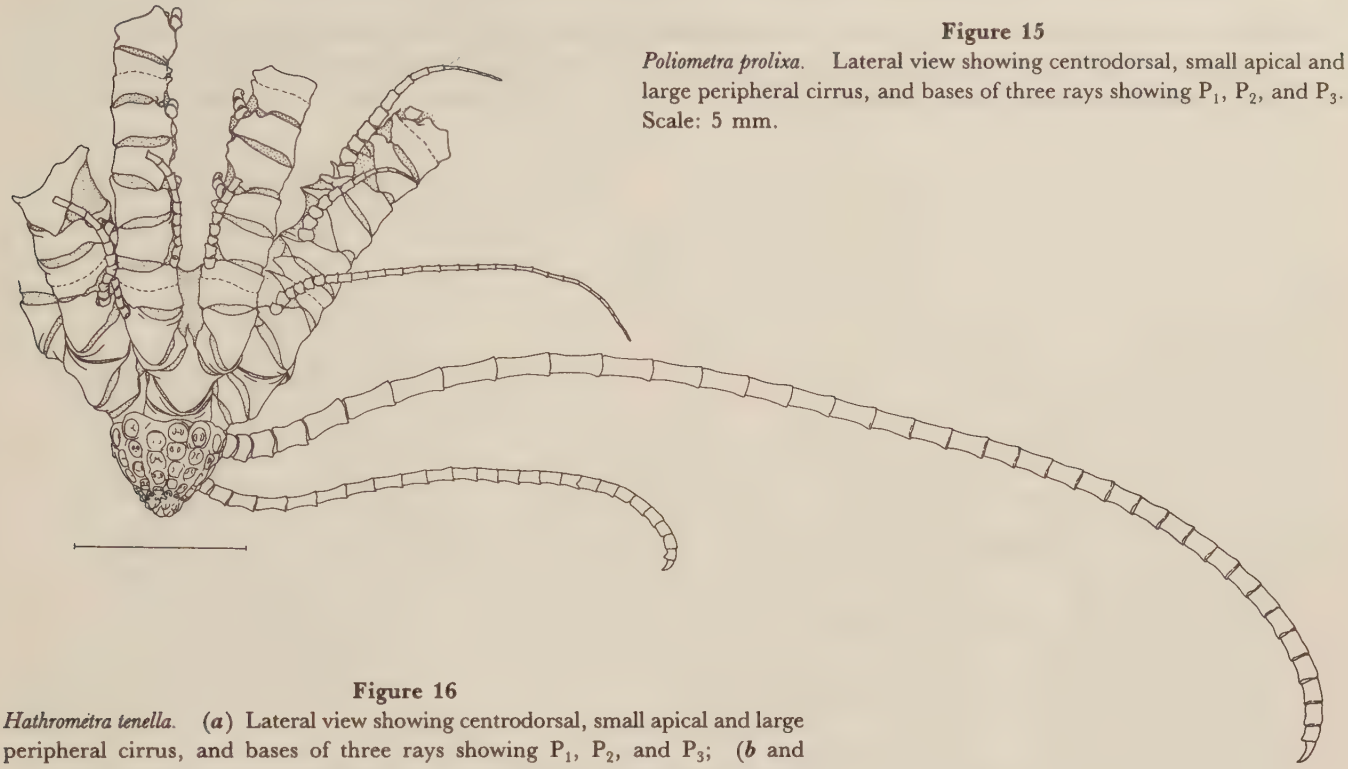
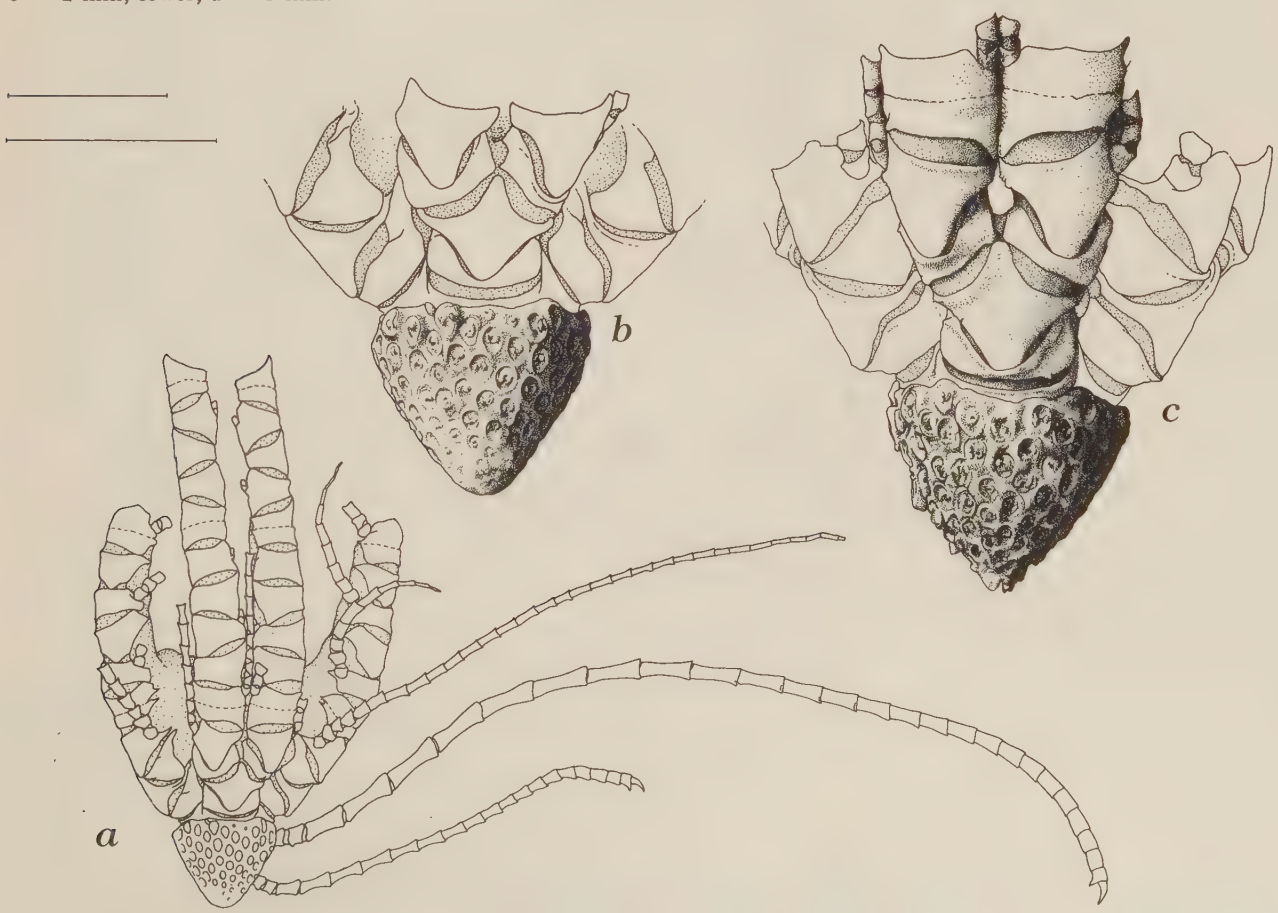


Figure 15

Poliometra prolixa. Lateral view showing centrodorsal, small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3. Scale: 5 mm.

Figure 16

Hathrometra tenella. (*a*) Lateral view showing centrodorsal, small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3; (*b* and *c*) Lateral views showing centrodorsal and bases of three rays. Scales: upper, *b–c* = 2 mm; lower, *a* = 5 mm.



14a(12b) Longest cirrus segments mostly 2.0–2.5 (maximum 3.0) times longer than their narrowest width; distal cirrus segments as long as or shorter than wide; P_1 3–6 mm long and composed of 11–15 segments; unknown north of the Blake Plateau ..... ***Trichometra cubensis* (*sensu stricto*) (Fig. 17)**

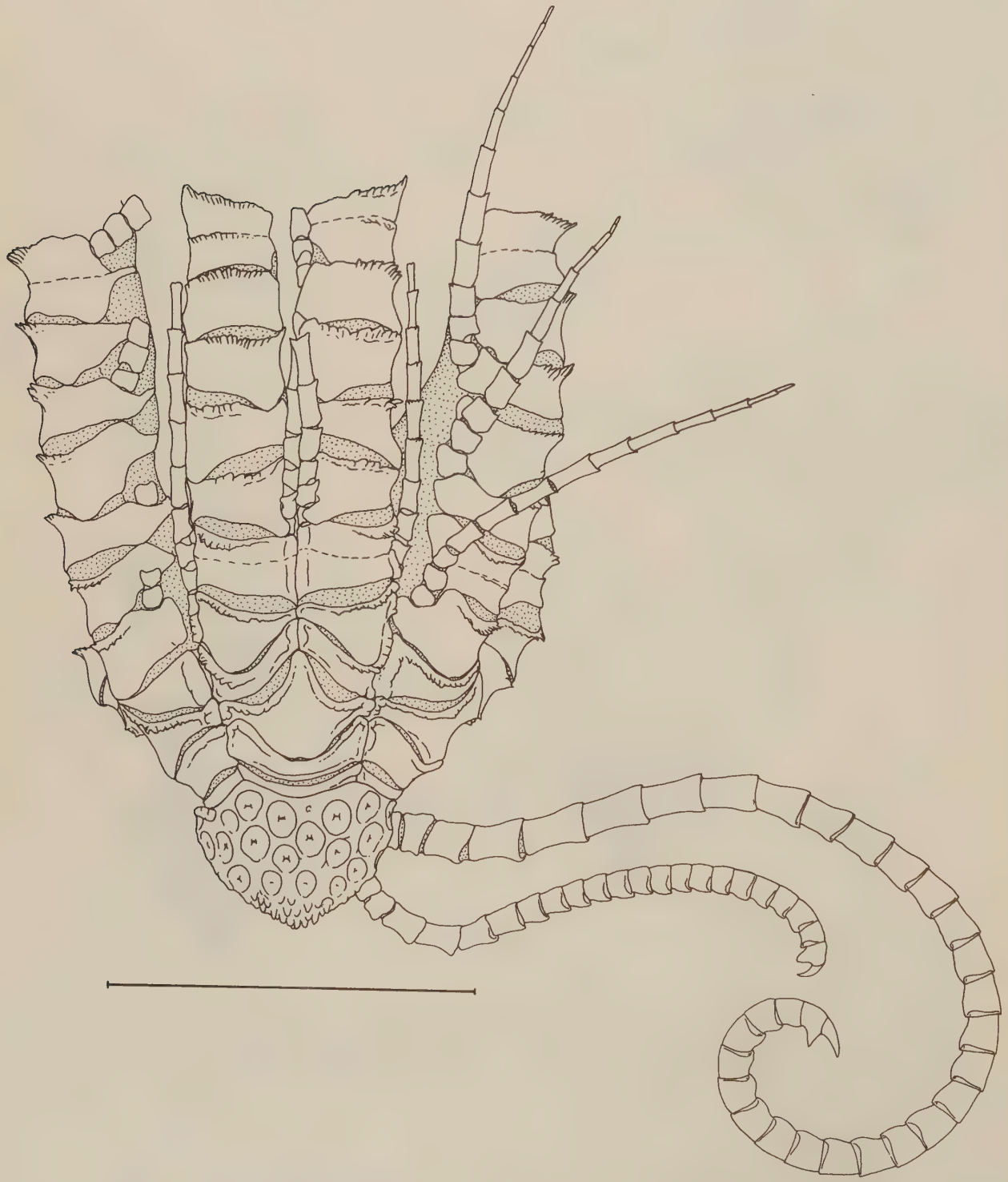


Figure 17

Trichometra cubensis (*sensu stricto*). Lateral view showing centrodorsal, small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3. Scale: 5 mm.

14b(12b) Longest cirrals mostly 3.0–3.5 (minimum 2.6) times longer than their narrowest width; distal cirrals usually slightly longer than wide; P_1 usually 7–11 mm long and composed of 16–23 segments; as far south as New England ..... ***Trichometra cubensis*** **(northern form) (Fig. 18)**

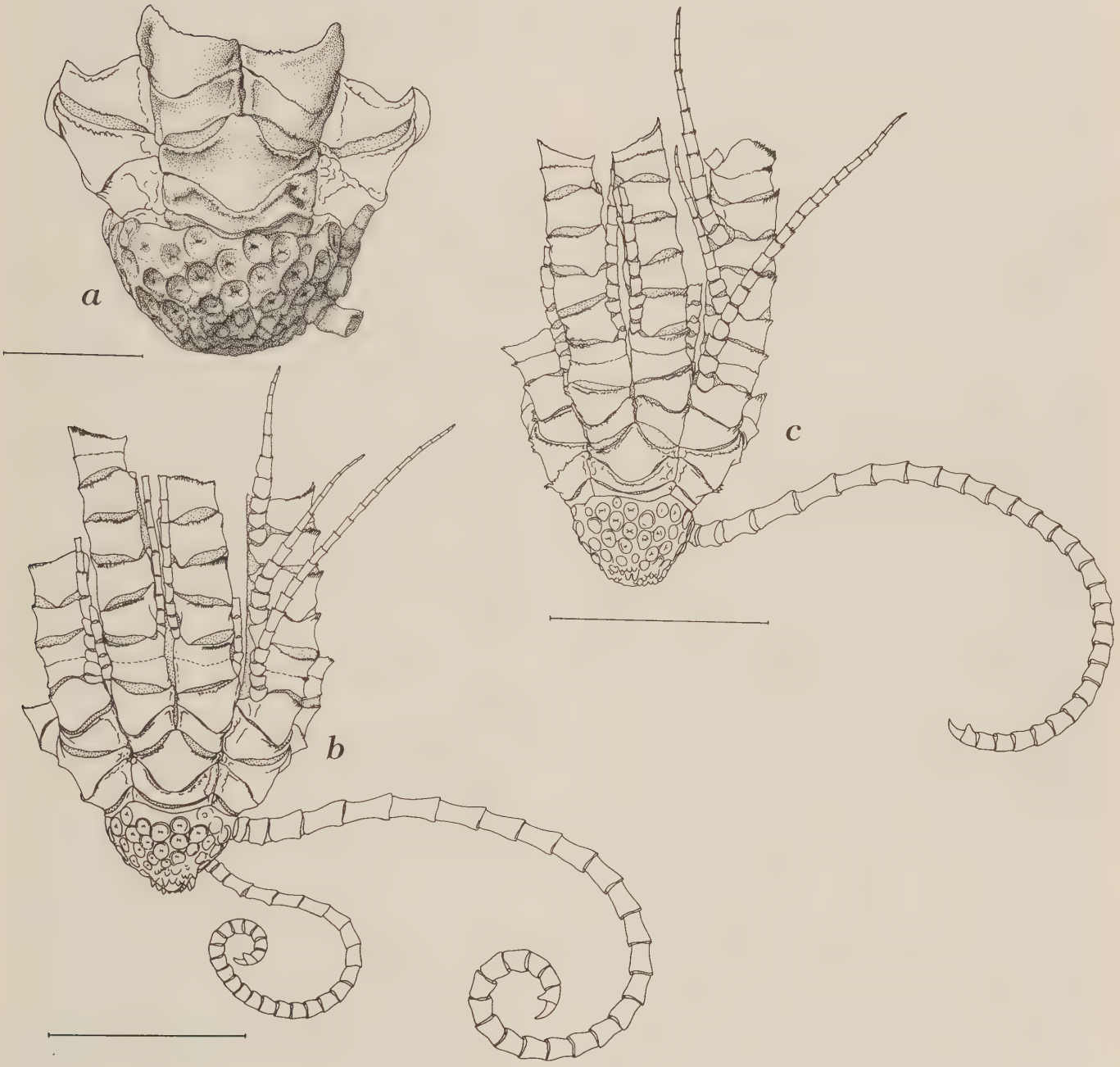


Figure 18

Trichometra cubensis (northern form). (*a*) Lateral view showing centrodorsal, cirrus bases, and bases of three rays; (*b*) Lateral view showing centrodorsal, small apical and large peripheral cirrus, and bases of three rays showing P_1, P_2, and P_3. (*c*) The same of another specimen (lacking small apical cirrus). Scales: *a* = 2 mm; *b–c* = 5 mm.

Annotated Systematic Checklist

This list follows the higher classification proposed by Rasmussen and Sieverts-Doreck (1978). Genera are arranged alphabetically within families. A new classification of the subclass Articulata has recently been proposed by Simms (1988). The only change that directly affects familial level taxa and below included here is the removal of the Atelecrinidae from the Paracomatulacea (probably returning it to the Antedonacea although the author does not specify). Geographic and bathymetric ranges include all published records plus data from additional specimens examined at the National Museum of Natural History (N.M.N.H.), Smithsonian Institution; Museum of Comparative Zoology, Harvard University; and Newfoundland Museum, St. John's, Newfoundland. Temperature and substrate data are from Clark and Clark (1967) and Clark (1970) except where indicated.

Class CRINOIDEA
Subclass ARTICULATA
Order BOURGUETICRINIDA

Family BATHYCRINIDAE*

***Conocrinus lofotensis* M. Sars, 1868**—Norwegian coast from lat. 58 to 70°N (possibly as far east as the Siberian Arctic, see Clark 1970); west of Ireland; south and west of the Faeroe Islands; between southeastern Greenland and Iceland; Davis Straits southward to Massachusetts; possibly off northern Florida. 140–3475 m.

Color—Crown yellow or grayish.

Habitat—Unconsolidated substrates: clay, mud, or combinations of mud and sand.

Remarks—This small sea lily has a stalk length to about 75 mm (usually to 50 mm) and a crown height (base of calyx to arm tips) to about 22 mm (usually 12–15 mm). Specimens from American waters were originally recognized as a distinct species (*Rhizocrinus verrilli* A. H. Clark), then reduced to varietal status as an extreme form of a continuum with *R. lofotensis* (Clark 1923). Gislén (1938) thought any distinction between the two doubtful and the two have since been treated as synonymous. Roux (1977) recognized the close similarity among the genera *Rhizocrinus*, *Conocrinus*, and *Democrinus* and placed *R. lofotensis* in the genus *Conocrinus* (Roux 1985). These three genera have been partly distinguished by calyx characteristics: *Rhizocrinus* and *Conocrinus* supposedly lack interbasal (and often interradial) sutures while *Democrinus* exhibits sutures between all calyx ossicles. However, Roux (1985) described *C. cabiochi* Roux with partial interbasal sutures and *D. parfaiti* (Perrier) with both interradial and interbasal sutures complete, irregular, partial, or not visible. He suggested that, while the three genera may not be synonymous, characters other than those offered by the calyx should be used to distinguish them.

The distribution of *C. lofotensis* along the east coast of the United States is uncertain. No records exist between northern Florida and Massachusetts. Because the Caribbean species *Democrinus conifer* (A. H. Clark) has been recorded from the Blake Plateau (see below), occasionally lacks interbasal sutures, and has calyx proportions overlapping those of *C. lofotensis*, the identity of the small, poorly preserved material of *C. lofotensis* from northern Florida remains unclear. The wide bathymetric range attributed to this species may also be due to misidentifications.

***Democrinus conifer* (A. H. Clark, 1909)**—Blake Plateau, Bahama Islands and Gulf of Mexico south along the coast of Central and South America, and the West Indies, to Brazil. 170–1750 m (chiefly 200–800 m). Most records are from the Straits of Florida south; the species was collected at a single R/V *Pillsbury* station off Jacksonville, Florida, on the Blake Plateau in 388–403 m (Meyer et al. 1978).

Color—Yellow or yellow orange with yellow arms.

Habitat—Unconsolidated substrates; mud or muddy sand.

Remarks—As mentioned under *Conocrinus lofotensis*, the distinction between the genera *Democrinus*, *Conocrinus*, and *Rhizocrinus* is unclear and the material of *C. lofotensis* from northern Florida may really represent this species.

Calyx proportions and stalk length are variable in *D. conifer* and the taxon may require subdivision. However, preliminary examination of a large number of specimens of this species and the sympatric *D. brevis* (A. H. Clark) and *D. robustus* (A. H. Clark) reveals no consistent differences between the three and they are here considered as synonymous.

Democrinus conifer reaches a much larger size than *C. lofotensis*; stalk length may exceed 280 mm and crown height reaches at least 78 mm. Large specimens sometimes appear to have ceased growing: newly developed thin proximal columnals may be absent so the topmost columnals are already squarish, and the calyx appears to be overgrown with secondary stereom that obscures interbasal sutures. The ultrastructure of the stalk was treated by Grimmer et al. (1984).

*Roux (1985) transferred *Conocrinus* and *Democrinus* (and *Rhizocrinus*) to the family Bourgueticrinidae but cited no reasons for the change.

Order COMATULIDA
Superfamily PARACOMATULACEA

Family ATELECRINIDAE

***Atelecrinus balanoides* Carpenter, 1881**—West of Ireland and southwest of the Faeroe Islands; Blake Plateau and Gulf of Mexico to Recife, Brazil. 550 to 1530 m. Specimens that may represent an undescribed species (see below) may have been collected as shallow as 178 m.

Color—White in preserved specimens.

Habitat—Unconsolidated substrates; mud or pelagic ooze. Photographs and observations made from submersibles [tentative identification, Messing (1985)] indicate bottoms apparently undisturbed by significant horizontal currents. Long delicate cirri (almost never retained in dredged material) act as outspread props; arms extend radially parallel to and just above the sediment with tips slightly upcurved. Usually dredged singly or in small numbers.

Remarks—Two bathymetrically allopatric forms exist. Most specimens collected shallower than 800 m have the following suite of characteristics: centrodorsal parallel-sided proximally, with weak interradial ridges and socket tubercles; basals slightly swollen interradially, if at all; profile of the external part of the radials forming an angle of 40–50° with a plane parallel to the centrodorsal base (normal to the oral/aboral axis); IBr_1 distolaterally cut away; axils rhombic or hexagonal with lateral margins converging proximally, not laterally thickened; adjacent axils well separated; synarthrial swellings weak or absent and, most consistently, Br_1 and Br_2 separated and rounded exteriorly (Fig. 7*a*: "*balanoides*" form).

Specimens collected primarily below 1000 m differ in the following respects: centrodorsal usually tapering from the base, with more prominent interradial ridges and socket tubercles; basals swollen interradially; radial/centrodorsal angle usually 30° or less; IBr_1 sometimes thickened distolaterally; axils hexagonal, with lateral margins parallel, thickened and ridge- or knob-like; adjacent axils usually in contact; synarthrial swellings moderate; Br_1 and Br_2 typically apposed, thickened and expanded or flattened exteriorly (Fig. 7*b*: "*helgae*" form).

The shallower-water form, including the type material of *A. balanoides*, has been collected between 800 and 900 m at a few stations in the Caribbean Sea; a few specimens of the deeper-water form have been collected in this depth range only on the Blake Plateau and off Brazil. The type of *A. helgae*, collected in 700 m off Ireland and synonymized with *A. balanoides* by A. M. Clark (1970), approaches the deep-water form in having some axils laterally thickened and Br_1 somewhat flattened exteriorly. Because most of the distinctions described above are not uniformly clear-cut relative to depth, we herein treat the two forms as infrasubspecific variants.

Several specimens collected from the Straits of Florida differ in several important respects and may represent an undescribed species. They bear up to 75 cirri in 15 closely crowded columns rather than ten, with much more prominent socket tubercles. None have been reported from the area covered by this paper.

Superfamily COMASTERACEA

Family COMASTERIDAE

***Comactinia echinoptera* (Müller, 1840)**—South Carolina; southeastern Florida; Bahama Islands and West Indies; Caribbean coast of Central and South America from the Yucatán Channel to Cabo Frio, Brazil (and, perhaps, to Isla de los Alcatraces off São Paulo). Found 2 to at least 92 m [possibly to 183 m; older deeper records (Clark 1931) are probably inaccurate]. Only one specimen has been collected in the area covered by this paper: off Raccoon Key, South Carolina.

Color—Centrodorsal and cirri white; radials, division series and arms reddish flecked with yellow; pinnules yellow. In preserved material, radials, division series and arms range from deep pink to very pale lavender; pinnules, ambulacra and disk tan or white. Ossicles retain lavender color after dissociation in sodium hypochlorite solution.

Habitat—Widespread but uncommon on reefs in the West Indies. It remains cryptic in crevices and under corals during the day and extends its longer arms to feed at night; the disk is rarely exposed. Arms form a monoplanar filtration fan normal to water movement with ambulacra facing one direction only (Meyer 1973; Macurda 1973, 1975).

Remarks—Large *C. echinoptera* develop significantly asymmetrical rays. Arms arising from the three rays closest to the mouth (located excentrically to one side of the disk) tend to be longer than arms arising from the two remaining rays. Ray asymmetry sometimes appears, albeit not as strongly, in *C. meridionalis*. See Messing (1978a) for a complete description.

***Comactinia meridionalis* (L. Agassiz, 1865)**—Cape Lookout, North Carolina to Surinam (possibly to São Paulo, Brazil), including the Bahama Islands, West Indies, and Gulf of Mexico. Found 3 to at least 373 m (possibly to 549 m). Localized, patchy shallow-water populations exist along the southeastern United States from the Carolinas to central Florida and off Central America, but the species seems to be limited to greater depths (>50 m) off southeastern Florida, the Bahamas, Gulf of Mexico, and West Indies.

Color—Yellow, sometimes with red (A. H. Clark uses "carmine," a vivid red) pinnules, often yellow-tipped; red, sometimes with yellow spots and orange to yellow pinnules

(sometimes red- or yellow-spotted or yellow-tipped); purple, sometimes with yellow- and purple-banded pinnules (after A. H. Clark, 1921). This list may include specimens referrable to *C. echinoptera* as A. H. Clark did not distinguish the two species of *Comactinia* in his monograph. Shallow-water specimens from the east coast of the United States have brown arms with narrow yellow bands, brown- and yellow-beaded pinnules, and the disk brown with yellow spots (from a photograph courtesy J. Miller, Harbor Branch Oceanographic Institute, Fort Pierce, FL).

Habitat—Rough hard bottoms and reefs, in rock crevices, sponges, or the undersides of corals (Meyer 1973; Messing 1985 and unpubl. observ.; J. Miller, pers. commun., Dec. 1988).

Remarks—*Comactinia meridionalis* exists in three reasonably distinguishable morphological forms. Size generally increases with increasing depth (Clark 1931; Messing 1978a). The shallow-water form (3–25 m; Carolinas to Central Florida and off Central America) is small; arm length usually does not exceed 45–50 mm. Specimens from the southeastern U.S. usually have more than XX cirri of 10–14 cirrals each. The cirri are more slender, longer in relation to centrodorsal diameter, and have their longest cirrals more elongated than in deeper water specimens. P_1 through P_3 bear relatively strong combs. This is the true *meridionalis* form corresponding to the type series. The larger, deeper water forms may represent a distinct species.

The second form occurs chiefly in 50–200 m in the Straits of Florida, Gulf of Mexico, and Caribbean Sea. Arm length reaches about 100 mm; cirri are fewer (usually XV–XVIII), stouter, usually with 9–11 cirrals. Combs appear on P_1 and P_2. A third, larger robust variant, *C. m. hartlaubi* Messing, has a similar distribution (although absent from southeastern Florida) but is characteristic of greater depths (200–400 m). Arms probably reach 250 mm in length; robust cirri usually number XX–XXX, with 11–14 short cirrals. P_1 through P_3 (sometimes also P_4) bear weak combs. See Messing (1978a) for a complete discussion of intraspecific variation.

Shallow-water specimens extend arms for feeding both day and night. Arms form a monoplanar filtration fan normal to wave oscillation with ambulacra facing one direction only. Meyer (1973) found specimens completely exposed on shallow reefs off Panamá.

***Comatilia iridometriformis* A. H. Clark, 1909**—Blake Plateau; northern Straits of Florida; Northwest Providence Channel, Bahamas. 256–686 m.

Color—Yellow.

Habitat—The following information is abstracted from Messing (1984, and references therein). This species is almost invariably collected with arborescent, azooxanthellate, bank-forming, scleractinian corals (e.g., *Lophelia prolifera*, *Enallopsammia profunda*) that contribute to dense thickets and extensive banks in the northeastern Straits of Florida, Blake Plateau and northeastern Gulf of Mexico. It occurs in dense (+ 15 individuals/0.25 m^2) patchy aggregations on dead coral, coral rubble, and low carbonate crusts adjacent to living coral thickets on elongated carbonate mounds (lithoherms) in the Straits of Florida. No specimens were observed clinging to living coral. Arms extend in a planar or shallow bowllike radial filtration fan.

Remarks—This species exhibits paedomorphosis, the retention of typically juvenile characteristics in an adult. Paedomorphic features include small size (maximum arm length ~30 mm), large centrodorsal cavity, large radial ossicles, apparently delayed metamorphosis of basals from a complete circlet into a rosette, incomplete pinnulation (i.e., the last few pinnules that normally develop in comatulids are absent in this species), extreme elongation of cirrals (relative to other Comasteridae), central mouth, coarse stereomic (skeletal) microstructure, and elongation of brachials. Messing (1984) suggested that paedomorphosis in *C. iridometriformis* is the result of progenesis [*sensu* Gould (1977)], that is, accelerated sexual maturation with retention of ancestral juvenile form.

Comatilia iridometriformis is the only internally brooding crinoid not found in middle or high southern latitudes. One or two of the most proximal genital pinnules (P_5, P_e, or P_6) may bear an enormously swollen gonad containing a single giant embryo or larva (1.4–1.6 mm long) that appears to lie free in the ovarian lumen. Advanced unreleased larvae have already developed a stalk, attachment plate, and calyx ossicles (all still embedded in the larva's globular body). Pentacrinoid postlarvae attached to cirri of adults and no larger than unreleased larvae, together with the species limited geographic range, suggest that a planktonic stage is absent or very brief.

P_2, P_3, P_4, P_b, P_c, and P_d are normally absent in adult specimens. P_2, P_4, and P_d occasionally occur, although neither all together on a single arm nor uniformly on all arms of an individual.

Superfamily ANTEDONACEA

Family ANTEDONIDAE

***Coccometra hagenii* (Pourtalès, 1867)**—Cape Lookout, North Carolina; Blake Plateau; Straits of Florida; Campeche Bank and Yucatán Channel. 14–1046 m. An extremely abundant species on the Pourtalès Terrace south of the Florida Keys, chiefly in 150–250 m; 567 specimens were collected in a single trawl at R/V *Gerda* station 1102 (Meyer et al. 1978). Only three specimens have been collected within the area covered by this paper: off Cape Lookout, North Carolina in 14 m (the shallowest record) and on the Blake Plateau in 805 and 1046 m (the deepest records).

Color—Pale greenish; young specimens with dark brown spots paired on arm bases but becoming confluent

distally; spots hardly apparent in adults (Pourtalès 1868, 1878); brownish (Nutting 1895, cited in Clark and Clark 1967). Some preserved specimens have strongly marked disks.

Habitat—Hard irregular substrates.

Remarks—Examination of extensive material collected by the University of Miami's R/V *Gerda* in the Straits of Florida indicates a slightly wider range of morphometric features than given in the most recent description of this species (Clark and Clark 1967), as follows: maximum centrodorsal diameter 3.1 mm (most specimens 2.2–2.8 mm); cirri XXVII–LXVIII, 8–25 (usually XLIII–LVIII, 15–19); P_1 of up to 43 segments; P_2 normally shorter and stiffer than P_1 with up to 21 segments and bearing a gonad; P_3 occasionally longer than P_2. Rarely, P_2 may lack a gonad and resemble P_1.

Dredged specimens typically retain their arms but lose their cirri.

***Comatonia cristata* (Hartlaub, 1912)**—Cape Lookout, North Carolina; Straits of Florida; Yucatán Channel. 14–580 m. All but three specimens were collected on the Pourtalès Terrace south of the Florida Keys in association with *Coccometra hagenii*, chiefly between 150 and 300 m. The only specimen known from the area covered by this paper was taken off Cape Lookout, North Carolina in 14 m.

Color—Yellow.

Habitat—Hard, irregular substrates. A single specimen was collected with coral rubble derived from arborescent, azooxanthellate, thicket-forming coral (*Lophelia prolifera*) in the northeastern Straits of Florida (Messing, unpubl.).

Remarks—A. H. Clark (1916, 1931) placed *C. cristata* in the Comasteridae on the basis of well-developed combs on the first pair of pinnules (and occasionally also P_2). All other morphological features (e.g., centrodorsal, division series, arms) indicate antedonid affinities. Messing (1981) pointed out that the comasteridlike combs are likely modifications of comb rudiments found in several antedonid genera and followed Gislén (1924) and Meyer (1972) in including the species in the Antedonidae.

Dredged specimens typically retain some cirri but lose their arms beyond the first or second syzygies.

***Hathrometra tenella* (Retzius, 1783)**—Scandinavia from Denmark to northern Norway; southwest of Ireland; Shetland Islands westward along the Faeroe Ridge to Iceland; southern Greenland; Davis Straits southward to off Chesapeake Bay. 28–1783 m (46–891 m off North America; tending to shoal to the north; off New England chiefly in 220–450 m). 2.0–13.9°C.

Color—Dark green dotted with white; cirri white; disk grayish (Clark 1921).

Habitat—Chiefly uncosolidated substrates: mud or mud and sand, sometimes in great abundance; Verrill (1882) reported over 10,000 specimens from a single dredge haul off Martha's Vineyard, Massachusetts.

Remarks—The distinction between *H. tenella* and *H. sarsi* (Düben & Koren, 1846) seems arbitrary. The latter, known chiefly from Iceland to Scandinavia, has been distinguished as smaller, with shorter cirri of fewer segments. Cirri of *H. sarsi* supposedly reach 17 mm long with up to 24 segments (Clark and Clark 1967; Clark 1970) while *H. tenella* bears cirri 25–35 mm long with 24–33 segments (Clark and Clark 1967). However, meristic and morphometric measurements for the two forms overlap widely and maximum reported arm lengths differ by only 10 mm (i.e., 100 vs. 110 mm). Re-examination of specimens collected off eastern Canada and New England (N.M.N.H. 11540, 11541) suggests a continuum; smaller specimens, identified by A. H. Clark as *H. sarsi*, bear cirri 11–12 mm long with 16–20 segments; larger specimens, identified by him as *H. tenella*, bear cirri 16–26 mm long with 14–30 segments. In one case, Clark identified both forms in the same trawl (*Albatross* stn. 2429).

Bathymetric and temperature ranges given above include records for *H. sarsi* from the northeastern Atlantic.

***Heliometra glacialis* (Owen, 1833)**—Wrangel Island (Arctic Ocean) westward to Spitzbergen and northern Norway (Finmark); off Norway (lat. 62–63°N) westward along the Faeroe Ridge to Iceland; Greenland, Hudson Bay, Labrador southward to off Cape Cod, Massachusetts; also in the North Pacific from the Okhotsk Sea to the Korean Straits (Clark 1970). 14–1358 m. −1.9 to +5.8°C (Clark 1970).

Color—Bright yellow, sometimes tinged with purple (Clark 1970).

Habitat—A variety of substrates including mud, sand, gravel, and stones; most frequently on gravel/sand and mud.

Remarks—The largest northern, cold-water comatulid. Arm length reaches 265 mm (350 mm in individuals from the northern Pacific); cirri to 90 mm (usually 60–70 mm).

***Poliometra prolixa* (Sladen, 1881)**—East of the Taimyr Peninsula westward to Novaya Zemlya; Spitzbergen; Norway north of lat. 62–63°N westward along the Faeroe Ridge to northern Iceland; Greenland; Baffin Bay and Davis Straits. 20–1960 m. −1.97 to +2.0°C.

Color—Arms brown to yellow; pinnules red to yellow; cirri white (Clark 1970).

Habitat—Chiefly soft mud or clay; sometimes on mud with sand or gravel.

Remarks—This species reaches North America only off Baffin and Ellesmere Islands in the Canadian Arctic.

***Trichometra cubensis* (Pourtalès, 1869)**—Morocco northward to the Faeroe Islands; south of Iceland; Davis Straits southward to Nova Scotia; southern Blake Plateau(?),

northeastern Gulf of Mexico and Bahama Islands southward to St. Vincent and Santa Marta, Colombia. 210–2432 m. 2.4–10°C. Shallower water material (~200 m) was collected chiefly off Arrowsmith Bank in the Yucatán Channel where strong northward geostrophic flow tilts isotherms upward to the west, bringing colder water into shallower depths along the Mexican side of the channel.

Color—Pale yellowish white.

Habitat—Often found clinging to arborescent cnidarians with narrow branches (e.g., antipatharians, some alcyonarians).

Remarks—In the northwestern Atlantic, two allopatric forms may represent distinct species. The southern form (including the type) occurs from the Bahamas and perhaps southern Blake Plateau southward and is included here for comparison. Cirrals are proportionately shorter (LW chiefly 2.0–2.5) and P_1 is shorter (3–6 mm) with fewer segments (11–15). The northern form is found from Nova Scotia northward and eastward. Cirrals are proportionately more elongated (LW chiefly 3.0–3.5) and P_1 is longer (7–11 mm) with more segments (16–23). The continuum in P_1 length and number of segments between the two forms is deceiving; specimens bearing minimum northern P_1-values are much smaller than specimens bearing maximum southern P_1-values.

We have not separated the two as distinct species because material identified as *Trichometra cubensis* from the northeastern Atlantic (Clark 1980) spans much of the range of variation found in both. Direct comparison of western and eastern Atlantic material has yet to be made.

Numerous small specimens identified as *Trichometra cubensis* collected on the Blake Plateau by the U.S. Fisheries Commission Steamer *Albatross* (e.g., N.M.N.H. 14700, 14707, 34608) represent an undescribed antedonid most easily distinguished by its more flexible pinnules composed of shorter, more numerous pinnulars with expanded spiny distal ends, and by Br_2 with a strong acute proximal margin.

***Zenometra columnaris* (Carpenter, 1881)**—Blake Plateau; northern Straits of Florida; northern Caribbean Sea (southwest of Haiti). A single record, originally catalogued as fragmentary but currently unidentifiable, exists from the Gulf of Mexico. 504 to 1034 m, chiefly 750–800 m. The Gulf of Mexico fragment was collected in 308 m.

Color—Unknown.

Remarks—The centrodorsal plate is truncated conical with weak interradial ridges in smaller specimens; in large specimens it becomes a five-sided cylinder with strong interradial ridges and a flat or excavated aboral pole.

Family PENTAMETROCRINIDAE

***Pentametrocrinus atlanticus* (Perrier, 1883)**—Blake Plateau; Martinique; Morocco; the Canary Islands and Azores north through the Bay of Biscay to Porcupine Bank off Ireland. 374–2115 m. In the western Atlantic, the possible depth range is 374–779 m with four of the five records shallower than 650 m. In the eastern Atlantic, the depth range is 650–2115 m with ten of the twelve records deeper than 1000 m.

Color—Preserved material white or pale tan with brown tegmen.

Habitat—Probably hard substrates dominated by sponges, alcyonarians, and azooxanthellate colonial scleractinians.

Remarks—This is the only five-armed species in the north Atlantic Ocean. Its morphology, distribution and relation to congeners were reviewed by Messing (1978b).

Species That May Occur Within the Area Covered by this Manual But Not Yet Reported

Order MILLERICRINIDA

Family HYOCRINIDAE

***Hyocrinus* (*Gephyrocrinus*) *grimaldii* Koehler & Bather, 1902**—Reported by Haedrich and Maunder (1984) in 1850–1875 m from Carson Canyon, Newfoundland. Reported elsewhere from the equatorial mid-Atlantic to the Canary Islands and Madeira.

Order BOURGUETICRINIDA

Family BATHYCRINIDAE

***Bathycrinus carpenteri* (Danielssen & Koren, 1877)**—Recorded from the deep basin of the Norwegian Sea as far west as eastern Greenland, and the Arctic Ocean as far east as the Laptev Sea, in 1360–2815 m (Clark 1970).

Order COMATULIDA

Family ANTEDONIDAE

***Antedon petasus* (Düben & Koren, 1846)**—Chiefly restricted to the coast of Norway in 10 to 326 m; a single specimen has been taken off southwestern Iceland (Clark 1970).

***Thaumatometra septentrionalis* A. H. Clark, 1918**—Known from Baffin Bay to Iceland. 2075–2623 m. 1.5 to 3.0°C (Clark and Clark 1967).

***Thaumatocrinus jungerseni* A. H. Clark, 1915**—Collected only between Iceland and Greenland. 823–2075 m (Clark and Clark 1967).

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Acknowledgments

Preparation of this manual was supported in part by a grant from the National Science Foundation to the Editorial Board of the "Marine Flora and Fauna of the Eastern United States."

The authors wish to express their thanks to the following individuals. Frederick M. Bayer (Smithsonian Institution) and the late Gilbert L. Voss (University of Miami) provided access to specimens collected by R/V *Pillsbury* and *Gerda*. Figures 6–12 and 14 are drawn from this material, now housed in the National Museum of Natural History. Access to additional specimens was provided by David L. Pawson (Smithsonian Institution); Robert Woollacott and Herbert Levi (Museum of Comparative Zoology, Harvard); Richard Haedrich (Newfoundland Museum); Linda Pequegnat (Texas A&M University); and A. Conrad Neumann (University of North Carolina, Chapel Hill). Ailsa M. Clark kindly granted permission to reproduce Figures 4, c and d, previously published in Clark (1970). Figure 6 was previously published in Messing (1978b), Figures 9, b to d, in Messing (1981), and Figures 10 and 11 in Messing (1978a). Figures 2, 8, 9, b to d, 10, and 11 were originally produced for the senior author's master's thesis (unpubl., University of Miami). The manuscript benefitted from reviews by David L. Meyer (University of Cincinnati), D. L. Pawson and M. R. Carriker (University of Delaware).

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Publication of the "Marine Flora and Fauna of the Eastern United States" is most timely in view of the growing universal emphasis on work in the marine environment and the critical need for precise and complete identification of organisms related to this work. It is essential, if at all possible, that organisms be identified accurately to species. Accurate scientific names of plants and animals unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been inadequately studied.

Charles G. Messing first became fascinated with marine invertebrates while an undergraduate at Rutgers University from which he graduated in 1970. His professional fate was decided when he was introduced to the invertebrate

collections at the University of Miami's Rosenstiel School of Marine and Atmospheric Science and the Smithsonian Institution during his first year of graduate study at the former. At the suggestion of Frederick M. Bayer in 1972, he began working on crinoids and has continued to do so since, despite occasionally straying to dabble in the biology of tanaidacean crustaceans. He received master's and doctorate degrees from the University of Miami and was subsequently awarded a Smithsonian post-doctoral fellowship to study crinoids at the National Museum of Natural History. Several years followed as a lecturer at the University of Miami (including a year as acting coordinator of the Undergraduate Marine Science Program) and as a freelance consultant and scientific illustrator. He was appointed assistant professor at Nova University's Oceanographic Center in 1990.

John H. Dearborn received his undergraduate training in Zoology at the University of New Hampshire and completed his M.S. degree at Michigan State University. His professional interests in marine invertebrates developed during summer employment with the U.S. Fish and Wildlife Service at Boothbay Harbor, Maine and field work for the Alaska Department of Fish and Game on Afognak Island. In 1958 he began doctoral studies at Stanford University and was presented with a unique opportunity to conduct field work on the ecology of marine invertebrates at McMurdo Sound, Antarctica. These early studies led to a lifetime passion for polar ecology, especially the biology of invertebrates of the Antarctic Shelf and crinoids and ophiuroids in particular. After completion of the Ph.D. degree he was awarded a National Science Foundation Postdoctoral Fellowship for echinoderm studies at the Museum of Comparative Zoology at Harvard. He joined the faculty at the University of Maine in 1966 and has been a Professor of Zoology there since 1976.

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